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COVER: Wilson's Snipe (*Gallinago delicata*). Illustration by Scott Rashid.

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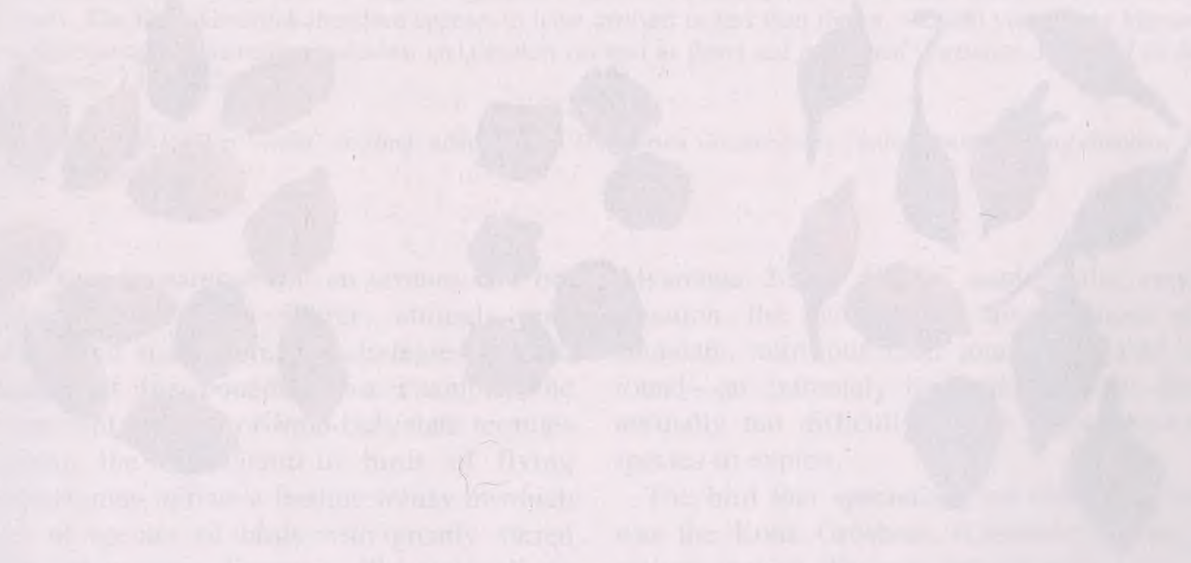
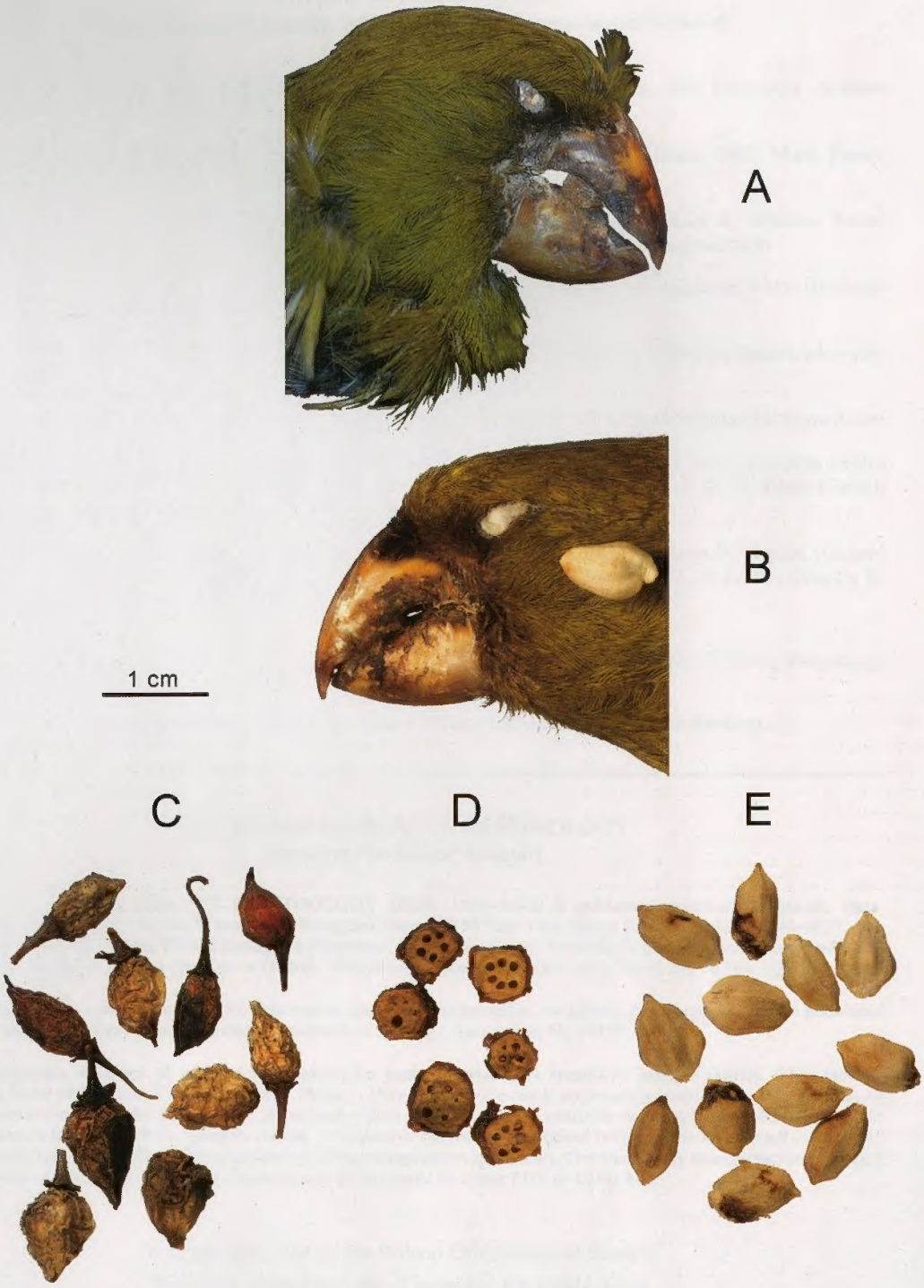
A HARD NUT ... EVOLUTION IN THE KONA GROSBEAK ... ALLY ABUNDANT FOOD SOURCE ... (*CARDUCS KONA*)





FRONTISPIECE. (A) Right side of head of a Kona Grosbeak (*Chloridops kona* BMNH 1939. 12.9.299) with a bisected naio fruit still held in the tomia; note the chipped ramphotheca of the mandible just in front of the fruit. (B) Left side of head of Kona Grosbeak (USNM 313565) showing heavy wear of the premaxillary tomium at the position where naio fruits were held when cracked (cleaned naio fruit on cheek for scale). (C) Dried naio (*Myoporum sandwicense*) fruits with pericarp; (D) Cracked naio fruits to show the cells that contained the minute seeds that were the actual food of the Kona Grosbeak; (E) Naio fruits with pericarp removed.

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A HARD NUT TO CRACK: RAPID EVOLUTION IN THE KONA GROSBEAK OF HAWAII FOR A LOCALLY ABUNDANT FOOD SOURCE (DREPANIDINI: *CHLORIDOPS KONA*)

STORRS L. OLSON[1]

ABSTRACT.—The Kona Grosbeak (*Chloridops kona*), last seen in 1892, was restricted to a small mid-elevation area on the leeward (Kona) side of the island of Hawaii. It was reported to feed almost exclusively on the fruits of the naio tree (*Myoporum sandwicense*), which are extremely hard, requiring a force of perhaps 400 newtons or more to open. The morphology of the skull and mandible of the Kona Grosbeak was accordingly much more modified for the hypertrophied adductor musculature needed to crack naio fruits than its closest relative, the Wahi Grosbeak (*Chloridops wahi*), which has been found as fossils on most of the other main Hawaiian islands. The Wahi Grosbeak is here hypothesized to have fed on less resistant seeds, such as those of the Hawaiian prickly-ash (*Zanthoxylum* spp.). Naio is widely distributed in diverse habitats in the Hawaiian Islands but its fruits were apparently an energetically viable food source only on relatively young (ca. 1200 year old) aa lava flows on the dry side of Hawaii, where the plants produce abundant flowers and fruit on a year-round basis. The Kona Grosbeak therefore appears to have evolved in less than the ca. 400,000 years since Mauna Loa became high enough to create a rain shadow and develop younger aa flows and associated vegetation. *Received 26 March 2013. Accepted 13 June 2013.*

Key words: *Chloridops wahi*, feeding adaptations, *Myoporum sandwicense*, naio, seed-cracking finches, Wahi Grosbeak, *Zanthoxylum*.

With the appearance of an evanescent but highly nutritious food source, animals may abandon their usual foraging strategies to take advantage of the bonanza. For example, the emergence of swarms of lipid-rich alate termites (Isoptera), the equivalent to birds of flying doughnuts, may initiate a feeding frenzy in which dozens of species of birds with greatly varied feeding adaptations become "flycatchers" in order to obtain the airborne prey (Olson and Alvarenga 2006). Here I explore the opposite situation, the evolutionary consequences of an abundant, nutritious food source available year-round—an extremely hard-shelled fruit—that is normally too difficult for any native Hawaiian species to exploit.

The bird that specialized on this food source was the Kona Grosbeak (*Chloridops kona*), an extinct species that was known only in a very limited area of the drier leeward side, the Kona district, of the "Big Island" of Hawaii. Its only close relative, the Wahi Grosbeak (*Chloridops wahi*, James and Olson 1991), is known solely from fossil remains from other islands of the

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Hawaiian Archipelago. Without knowledge of this fossil relative, the distribution and adaptations of the Kona Grosbeak could probably not be successfully interpreted. The first part of this paper is therefore a comparative analysis of these two species, to the extent that their adaptations can be extrapolated from the paleontological and anatomical evidence, followed by a review of the botanical and geological conditions that gave rise to the unique environment leading to the evolution of *Chloridops kona*.

DISTRIBUTION OF THE KONA AND WAHI GROSBEAKS

Among all the extinctions of passerines that took place in the Hawaiian Islands, the guild of finch-like drepanidines was disproportionately affected, with at least 11 species becoming extinct prehistorically (James and Olson 1991, 2005, 2006) and another 6 becoming extinct since 1891, leaving only the Palila (*Loxioides bailleui*) and the Laysan and Nihoa finches (*Telespiza cantans*, *T. ultima*) still extant, all three of which were much more widely distributed in the past (James and Olson 1991). Seven finch-billed genera vanished in the process: *Orthiospiza*, *Xestospiza*, *Psittirostra*, *Dysmorodrepanis*, *Chloridops*, *Rhodacanthis*, and *Melamprosops*.

Among these, the species of *Chloridops* had the largest, heaviest bills, and presumably fed on larger or harder seeds than the other finch-like genera. The King Kong Grosbeak (*Chloridops regiskongi*, James and Olson 1991), known only from fossils from Oahu, was the largest, but its bill shape was quite different from other species of *Chloridops* and no potential food source has yet been hypothesized for it. *Chloridops wahi* (James and Olson 1991) was originally described from Oahu, with referred specimens from Maui. Fragments of uncertain specific identity were also known from Kauai, and excellent material collected later showed that the Kauai population was referable to *C. wahi* as well (Burney et al. 2001). From its presence on Maui, it is quite likely that *C. wahi* once occurred on Molokai, where species diversity in fossil deposits is low because of ecological limitations (Olson and James 1982), and on Lanai, where the fossil record is very scant (Dove and Olson 2011). A species similar to *C. wahi*, but smaller, is known from Maui but remains unnamed (James and Olson 1991).

The only historically known species of the genus is the Kona Grosbeak (*Chloridops kona*), which was first collected in June 1887 and named as a new genus and species by Scott B. Wilson (1888). The last specimen was collected in September 1892 and the species was never seen again, so that it was known to science as a living bird for only 5.5 years (Olson 1999) and was apparently unknown to Polynesian residents. The plumage was entirely dull olive green, therefore, it would not have been prized for featherwork even if it had been known to native birdcatchers. The species is characterized by its enormous conical bill, but the body of the bird was actually rather small by comparison. This may fit the pattern found by Benkman (1991) that seed-eating finches on islands have smaller bodies relative to those of continents.

All authors who encountered the Kona Grosbeak remarked on its very restricted distribution, estimated to have encompassed no more than about 10 km^2, centered on the volcanic cone of Puu Lehua in the North Kona District on the leeward slopes of Mauna Loa on the island of Hawaii. Although bones of some extinct passerines have been collected in lava tubes on Hawaii, the collections are by no means comprehensive and no remains of Kona Finch or any of the other larger finches have as yet been found. It is therefore quite conceivable that the Wahi Finch could have been present and perhaps more widely distributed on the Big Island than was the Kona Finch, as there was probably little or no competition between them for food, as will be seen.

FOOD AND FEEDING ADAPTATIONS OF KONA AND WAHI FINCHES

Apart from moth caterpillars and probably other insects fed mainly to the young, the Kona Finch appears to have fed almost exclusively on the extremely hard fruits of the naio or bastard sandalwood (*Myoporum sandwicense*; Myoporaceae). These fruits, ranging from 2–9 mm in size, include a "bony" endocarp containing 4–10 cells with one seed per cell (Wagner et al. 1990). The fruits are covered with a pericarp, leathery when dry (Frontispiece C), that was doubtless the source of the exudate that built up around the cutting edges of the bill of the Kona Grosbeak and that still persists in most specimens (Frontispiece A, B). A sample of 12 fruits, with pericarp removed (Frontispiece E), that I collected from the feeding area of the grosbeak, measured 4.0–6.1 (mean 4.9) mm X 8.1–9.4 (8.6) mm. Similar fruits with dried

FIG. 1. (A) Fossil seeds of Hawaii prickly ash (*Zanthoxylum hawaiiense/kauaense*), a likely food source for the fossil Wahi Finch (*Chloridops wahi*) that occurred in the same fossil deposits on Kauai (two cleaned naio fruits on right); B, C, plastic casts showing the ramphotheca in a specimen of Kona Grosbeak (*Chloridops kona* AMNH 453677): rostrum in ventral view (B) and mandible in dorsal view (C).

pericarp could only be opened with wire-cutting pliers and usually contained 4–5 cells, sometimes with one of them being much larger than the others (Frontispiece D). The amount of food to be extracted from each cell would have been very small, the assumption being, however, that it must have been exceptionally nutritious. Munro (1944) described these seeds as appearing "maggot-like" when found crammed by the hundreds in the crops of specimens he prepared. The mechanism for opening the naio fruit would not have been comparable to the two sharp edges of wire-cutting pliers but rather involved the cutting surface of the upper tomium only against the more anvil-like pad of the opposing mandibular surface (Fig. 1B, C).

Some indication of the tremendous physical effort required to open these fruits is evidenced by the fact that the incessant cracking noise made by feeding birds could be heard at some distance and provided the means by which this usually silent species could be located by collectors. The birds were said to feed most of the day (Olson 1999) and Perkins (1893:105) thought that the species' whole existence could be summed up by the words "to eat," which may be an indication of the amount of effort needed to sustain itself solely from the exertion of cracking naio fruits.

There is ambiguous evidence that the cracking process was subject to "handedness," or more properly "lateralization," of the mandibles. Munro (in Olson 1999:8) mentioned two birds collected 10 October 1891 that "had a piece of aaka [naio] clenched in the bill and we left them there after skinning, in each it was held in the left side between the edges of the mandibles just above the tooth of the lower mandible." These specimens were not located although one specimen in the Natural History Museum, London (BMNH 1939.12.9.299) had a piece of naio fruit in the right side of the jaws (Frontispiece A). This had been cut crosswise exposing the seed cells as in Frontispiece D, and was held with the cut surface facing posteriorly. In a few skin specimens of *C. kona*, the tomia on one side appeared to be more worn or notched than the other, but in most specimens such differences were not detectable. Using the same side for a repetitive task may impart increased neuromuscular efficiency as well as causing hypertrophy of muscles on one side to give greater strength to open a slightly larger or harder fruit.

Because the much more widespread Wahi Grosbeak (*Chloridops wahi*) is known only from fossils, we can only surmise what its diet may have been. A good indication, however, comes from fossil lake sediments on southern Kauai where bones of *C. wahi* occur together with seeds of the tree *Zanthoxylum hawaiiense/kauaense* (Burney et al. 2001). The specific distinctness of these taxa is uncertain and their seeds, which are among the most abundant plant macrofossils at the site, cannot be distinguished from one another (Burney et al. 2001). The seeds are blackish with a sculpted surface and are about 7–8 mm in diameter (Fig. 1A), a size that could be accommodated by the width of the groove in the mandible of *C. wahi*. Fresh seeds appear to have high lipid content (T. B. Smith, in litt., 8 Nov 2000).

Zanthoxylum (Rutaceae), species of which occur throughout the main Hawaiian islands, is a very widespread genus of about 200 species found in tropical America, Africa, Asia, Australasia, and the Pacific and in temperate eastern North America and eastern Asia (Porter 1976). Its seeds are probably fed upon by large finches wherever the two occur together. For example, in the Galapagos, "the hard, black seeds of *Zanthoxylum fagarae*, ~2–3 mm in diameter, were frequently eaten" only by the largest of the Galapagos finches, *Geospiza magnirostris* (Bowman 1961:26).

The hardness of five seeds from two herbarium specimens identified as *Zanthoxylum kauaense* was tested by the same equipment used by Smith (1990) and ranged from 100–265 newtons (N). This is within or considerably in excess of the range of force required to crack the hardest seeds fed upon by large-billed morphs of the African Black-bellied Seedcracker (*Pyrenestes ostrinus* Estrildidae) (Smith 1990), a smaller species than the Wahi Grosbeak. On the other hand, two seeds

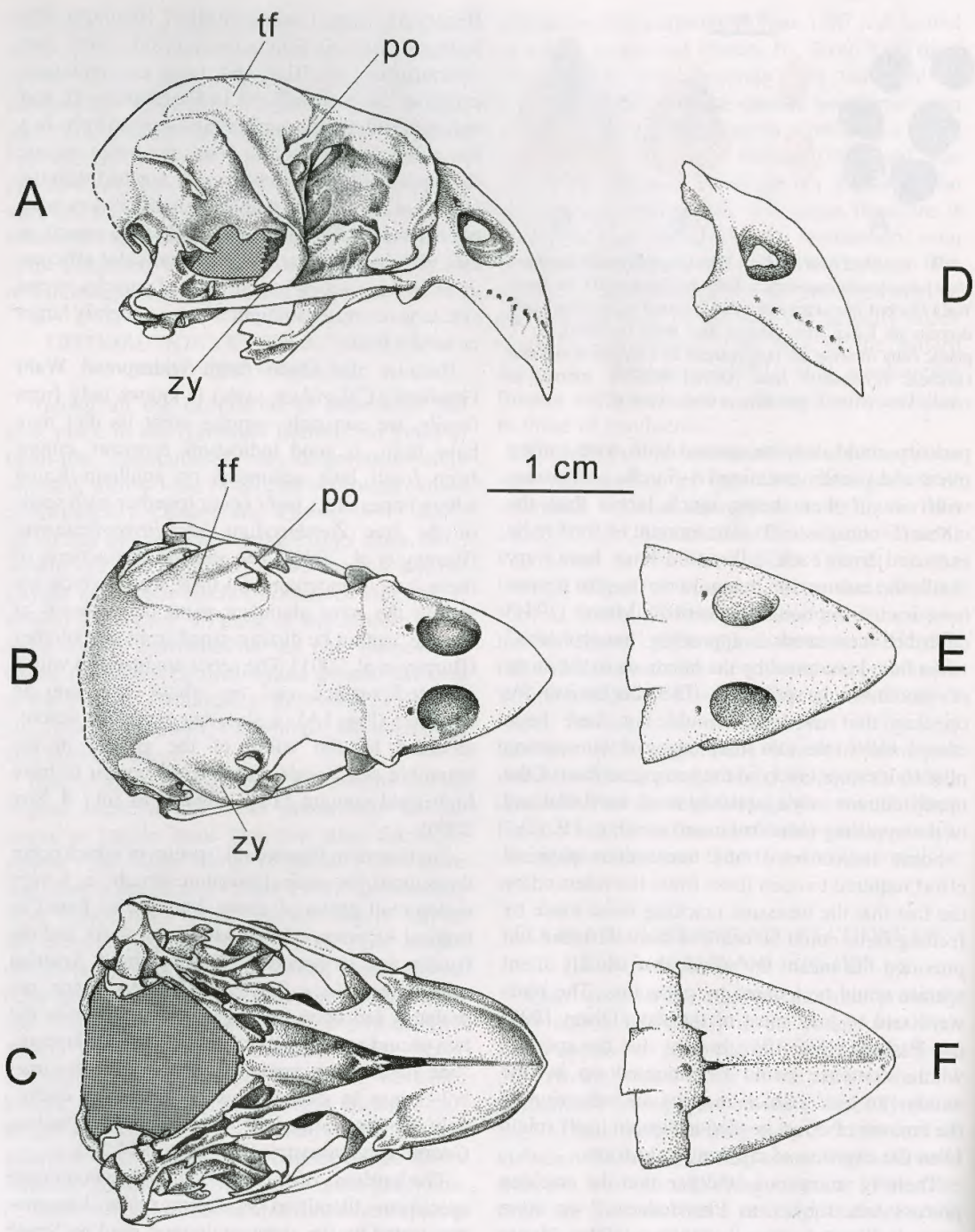

FIG. 2. Skulls and rostra of *Chloridops*. Left column: Kona Grosbeak (*C. kona* AMNH 453677) in right lateral view (top), dorsal view (middle), and ventral view (bottom). Right column: same views of the rostrum of Wahi Grosbeak (*C. wahi* USNM unnumbered). po, postorbital process; tf, temporal fossa and adductor muscle scars; zy, zygomatic process.

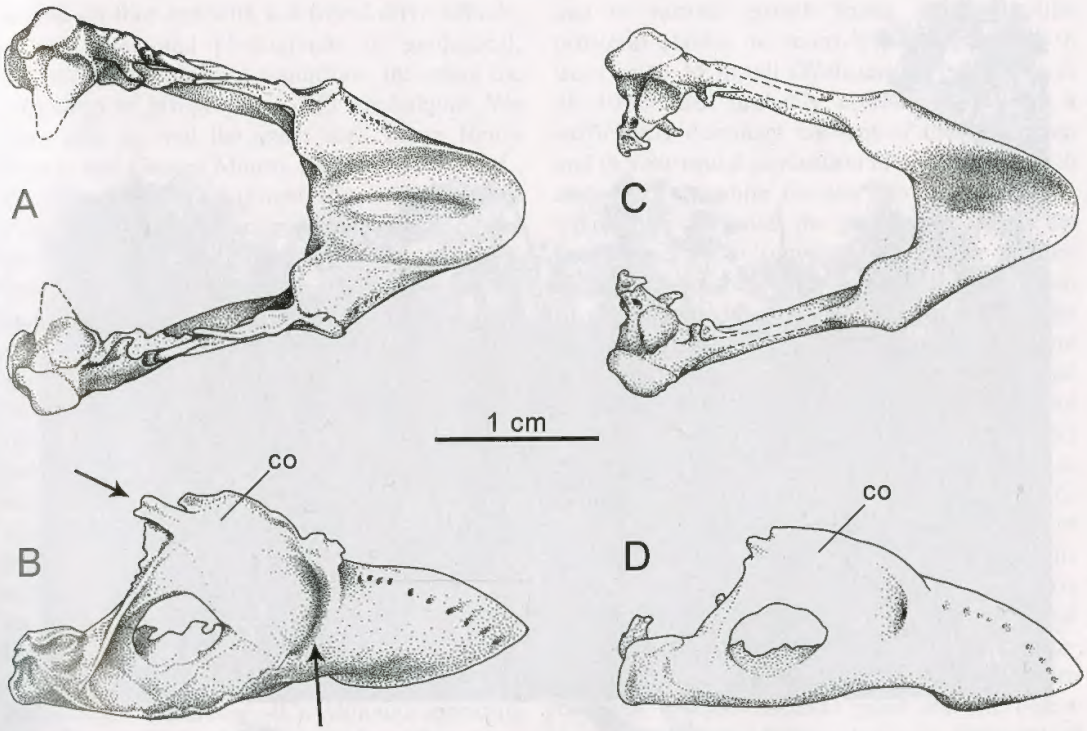

FIG. 3. Mandibles of *Chloridops*. Left column: Kona Grosbeak (*C. kona* AMNH 453677) in dorsal view (top) and right lateral view (bottom). Right column: same views of Wahi Grosbeak (*C. wahi* USNM 524868, Kauai). co, coronoid process; arrows indicate features discussed in the text.

of naio (*Myoporum sandwicense*) that I collected in 1999 were too hard to be cracked by the testing equipment and were estimated to require fracture forces in excess of 400N (T. B. Smith, in litt., 2 Nov 2000).

Examination of the skull and mandible of *Chloridops kona* (Figs. 2, 3) shows that they are massively adapted for crushing. The adductor muscle scars in the temporal fossa are exceptionally extensive and deep and especially notable is the huge zygomatic process, which extends ventrally to the level of the quadratojugal bar and is situated so far anteriorly as almost to abut the postorbital process. The zygomatic is also the site of origin of muscles of the adductor complex. Nothing comparable to the condition of *C. kona* exists even in the largest and heaviest-billed of the Galapagos finches, *Geospiza magnirostris* (Bowman 1961, pl. 9). Compared with *C. wahi*, the premaxilla of *C. kona* is foreshortened and more rounded, less triangular (Fig. 2A–C), with more curved tomia (Fig. 2C).

The mandible of *C. kona* is likewise much more massive than that of *C. wahi* (Fig. 3), the postdentary portion being much deeper, the coronoid process much higher, the anterior margin of the muscle insertion much deeper where it meets the mandibular symphysis (dentary), forming a high curved ridge that is hardly indicated in *C. wahi*. The tendinous attachment at the tip of the coronoid process is also much more ossified in *C. kona*. The trough in the mandibular symphysis is wider in *C. wahi* than in *C. kona*, doubtless reflecting the difference in the size of the seeds that they handled. Although this trough does not play a role in the actual cracking, it is where the seed is held and manipulated by the tongue both before and after the seed is opened.

In summary, the Kona Grosbeak was highly adapted for exerting tremendous crushing/cutting forces in order to be able to open the excessively hard fruits of naio that were nearly its sole food. It may have been capable of exerting greater force than any other known finch-like bird, including those that are considerably larger.

GEOLOGY AND ECOLOGY OF KONA GROSBEAK HABITAT

From 3–5 March 1999, I made surveys, with T. Casey and J. Crummer, of former Kona Grosbeak

FIG. 4. (A) Habitat of Kona Grosbeak (*Chloridops kona*) near Puu Lehua, Kona District, island of Hawaii, in the area where the species was collected in 1887–1892; note the rugged, boulder aa lava flow; the scrubby trees are mostly naio (*Myoporum sandwicense*), the main food source of the Kona Grosbeak. (B) Naio plant from the same area showing the abundant fruit and flowers that are present year-round at this locality. (C) Robust growth form of a nearby naio tree (behind the seated person) growing on a pahoehoe flow; this tree bore no fruit or flowers at the time (Mar 1999) when nearby naio trees on aa flows were fruiting abundantly.

habitat on foot and with a 4-wheel drive vehicle, taking notes and photographs of geological, edaphic, and biological conditions, including the phenology of *Myoporum* in different habitats. We were able to visit the exact sites where Henry Palmer and George Munro, followed by R. C. L. Perkins collected Kona Grosbeaks, as delimited in Olson (1999). Those collectors all described the birds as feeding on the naio growing on "clinker" flows, by which it became obvious that they meant large, rugged masses of bouldery aa lava (Fig. 4A). Here the predominant vegetation was naio (*M. sandwicense*), interspersed with mamane (*Sophora chrysophylla*), koa (*Acacia koa*), aalii (*Dodonaea viscosa*), a few ohia (*Metrosideros polymorpha*), pukiawe (*Leptecophylla tameiameiae*), and uulei (*Osteomeles anthyllidifolia*). Although of a scrubby growth form, all the naio trees here were reproducing abundantly and bore copious flowers and fruits in every stage of seed set (Fig 4B). Interestingly, on nearby pahoehoe lava flows, which sustained pasture suitable for cattle, naio trees were scattered but grew taller, with straight trunks (Fig. 4C). Although appearing more robust, these trees did not bear flowers or fruit at the time of my visit in March 1999.

On the coarse aa "clinker" there was little or no soil development or water retention. This, the leeward Kona side of Hawaii, is in the rain shadow of Mauna Loa and receives far less precipitation than the windward side, although conditions here are often overcast or foggy, which is why the area is famed for growing coffee. The naio trees of the aa flows thus probably grow under less than ideal conditions of water and mineral availability; perhaps such stress keeps them in a constant state of fecundity. My visit was in March, whereas the collectors of Kona Grosbeaks were present in July to October 1891 and 1892, when birds were actively feeding on abundant fruit. Thus I assume that naio trees on the aa flows are probably reproducing on a year-round basis.

Another factor influencing the environment here is the relatively young age of this aa "clinker", which is referred to by the U.S. Geological Survey Hawaiian Volcano Observatory as the "Honey Bee" flow (flow ID 441). The average of two radiocarbon dates from this flow was 1268 ± 49 years (averaged using Quaternary Isotope Laboratory CALIB Program—Frank A. Trusdell, in litt., 22 Jan 2008).

Naio is found throughout the main Hawaiian Islands from coastal strand to subalpine forest and in various growth forms from vine-like prostrate shrubs, to many-branched bushes, to trees up to 15 m tall (Webster 1951, Wagner et al. 1990). But probably nowhere is it both a sufficiently dominant element of the vegetation and in year-round production of abundant fruit to make it worthwhile for any bird to evolve the adaptations to crack the stony fruit. Only the special set of circumstances found on the relatively young aa lava flows at mid-elevation in the rain shadow of Mauna Loa provided the growing conditions for naio to become abundant and produce year-round fruit. It is likely that *Chloridops wahi*, found essentially throughout the rest of the Hawaiian Islands, was the direct ancestor of *C. kona*. There is no historical or paleontological evidence for the existence of *C. kona* outside the Kona districts of the island of Hawaii. The Kona Finch must have evolved its naio-feeding adaptations since Mauna Loa reached an elevation to cast a rain shadow and produce younger aa flows with suitable vegetation (the oldest dated rocks of Mauna Loa are between 100,000–200,000 years and the oldest subaerial portion of the volcano is estimated at 400,000 years; U.S. Geological Survey 2006). Eventually the environment of suitable "clinker" flows for Kona Finches must have changed through erosion, soil development, and vegetational succession such that they no longer presented sustainable conditions, necessitating a move of the birds to younger flows.

Populations of Kona Finch were probably always low in number and had doubtless been reduced by introduced disease, such as avian pox, by the time the species was discovered. All that is likely to have remained from 1887–1892 would have been a few scattered family groups and lone individuals so that it is not surprising that Palmer, Munro, and Perkins observed that there was much suitable habitat in which there were no birds present (Olson 1999).

CONCLUSION

We know nothing of breeding in the Kona Grosbeak except that birds evidently did not breed from July through October (Olson 1999). Perhaps fat buildup combined with cyclical outbreaks of moth caterpillars as a protein source for the young, were what allowed sufficient time off from eating to engage in pairing, mating, egg and nest building, and rearing offspring. Extreme morphological specialization for feeding on naio

fruits would not have prevented the Kona Grosbeak from expanding its niche to encompass other types of seeds. But to do so would have increased search time, travel time between food patches, and may have brought on competition with other large-billed finches such as *Chloridops wahi*. Feeding on naio fruits may have required a full-time commitment for the birds to be able obtain sufficient energy to make the effort worthwhile. Thus, most of the existence of the species *Chloridops kona* may have consisted of the numbing repetition of cracking rock-hard naio fruits; what we can now see of its adaptations reflect the thousand natural shocks that bone is heir to.

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EXTRA-PAIR MATING AND SEXUAL SELECTION ON MALE TRAITS ACROSS POPULATIONS

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ABSTRACT.—Research on sexually selected male traits has intensified over the last two decades and there are now many species of birds for which male traits associated with extra-pair mating success have been identified. Some of the more commonly studied species have been examined in multiple populations; however, there is often little consistency in results between studies. In paired analyses of Tree Swallows breeding in Wisconsin, we found that successful extra-pair sires were more experienced breeders, heavier, had fewer lice holes in their feathers, had longer wings and tended to be in better condition than the male they cuckolded. Our results are similar to those from a population of Tree Swallows studied in Ontario but differ from a population studied in British Columbia. Such variation among populations may arise if environmental heterogeneity influences the information content, reliability, or importance of particular male traits as signals of male quality. Taking these factors into consideration will help us understand how selection on male traits varies between populations and the role of extra-pair mating in sexual selection. *Received 19 July 2013. Accepted 24 September 2013.*

Key words: extra-pair mating, sexual selection, *Tachycineta bicolor*, Tree Swallow.

Extra-pair paternity occurs in many species of birds (Griffith et al. 2002) and can increase the opportunity for sexual selection (Whittingham and Dunn 2005). Hundreds of studies have searched for phenotypic traits that are associated with extra-pair mating success, as these traits might reflect the genetic quality or competitive ability of males. However, only about half of the studies have found traits related to extra-pair mating success (Akçay and Roughgarden 2007). If there are consistent patterns, then the strongest seem to be that successful extra-pair sires are older, in better condition, larger or more ornamented (reviewed in Griffith et al. 2002, Akçay and Roughgarden 2007). In the past, most studies of sexual selection have focused on only one population, and assumed that the level of extra-pair mating, as well as the strength and targets of sexual selection are generally consistent between populations of the same species. However, a growing number of studies, of the same species in multiple populations, are showing that the level of extra-pair paternity can vary widely among populations (Sardell et al. 2010), suggesting that researchers may need to examine this assumption in more detail.

Several factors may be contributing to the lack of consistent identification of traits that are sexually selected through extra-pair mating. First, traits selected through extra-pair fertilization success may not be the same traits selected through within-pair fertilization success (Cleasby and Nakagawa 2012). For example, in one population of European Pied Flycatchers (*Ficedula hypoleuca*), UV reflectance in the white wing patch was related to greater within-pair paternity, whereas male age was associated with siring more extra-pair young (Lehtonen et al. 2009). Thus, we need to consider that mate choice is often context-dependent, and thus, females may respond to different traits as signals of male quality in different situations (within-pair or extra-pair).

Second, some studies, even of the same species, do not analyze the same traits in similar ways. For example, many studies examine correlations between male traits and fertilization success across all males in the population, rather than pairwise between extra-pair males and the within-pair male that they cuckold. The population-wide analysis assumes that individuals seeking extra-pair matings (either female or male) have similar access to all potential mates in the population. However, studies that have been able to assign sires to most or all of the extra-pair young show that extra-pair mating often occurs between territorial neighbors (or within one territory; reviewed in Sardell et al. 2010). This suggests that extra-pair mating and selection on male traits is often spatially limited (Webster et al. 2001). In addition, estimates of total reproductive success may be biased by the incomplete sampling of males in the population (Sardell et al. 2010). Therefore, the pairwise analysis is probably a more direct and powerful test of differences in traits between extra-pair and within-pair males.

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Third, studies of different populations of the same species often do not take into consideration the environmental heterogeneity between populations that could potentially affect the expression of male traits (e.g., Hill et al. 2002) or the information content and reliability of a particular trait as a signal of male quality (Schluter and Price 1993).

In this study we used paired analyses to examine male characteristics specifically associated with extra-pair fertilization success in Tree Swallows (*Tachycineta bicolor*) breeding in Wisconsin. We compare our results to other populations studied in Ontario and British Columbia, and we review studies of other avian species studied in multiple populations that have found male characteristics specifically associated with success as extra-pair sires.

METHODS

Study Area and Species.—We have studied Tree Swallows at the University of Wisconsin-Milwaukee Field Station near Saukville, Wisconsin (43° 23′ N, 88° 01′ W) since 1997. The study area consists of 6 ha of fields that have 88 nest boxes, located in two grids 600 m apart. Within grids, nest boxes are 40 m apart along a row and 28 m apart on the diagonal between rows; which is similar to natural densities of breeding Tree Swallows (Robertson and Rendell 1990). Tree Swallows are small (~20 g), socially monogamous migrants that nest in secondary tree cavities but readily breed in nest boxes (Robertson et al. 1992). There are typically 4–6 eggs per clutch that are incubated solely by the female, and there is one brood per year in our population.

Adult sex was determined by the presence of a brood patch or cloacal protuberance. Males attain the definitive adult blue-green plumage during their first breeding season and natal philopatry is less than 1%, thus, it was not possible to determine the exact age of males in our population. Therefore, in our analyses we used breeding experience, and not age, although they are most likely highly correlated. All males breeding in our population were banded beginning in 1997, so adult males in this study were categorized as experienced breeders if they had been captured in a previous year (banded) and inexperienced breeders if they were new to our population (unbanded; e.g., Robertson and Rendell 2001). Tree Swallows have an average life span of 2.7 years and usually breed only 1–2 years (Robertson et al. 1992).

All adults were caught inside nest boxes when nestlings were 4–8 days old. Each adult was weighed (±0.1 g), measured (wing, tarsus, and keel length with digital calipers ± 0.1 mm) and marked with a U.S. Fish and Wildlife Service band on the right leg and a colored plastic band on the left leg. Body mass was not related to capture date (r^2 = 0.019, P = 0.19, n = 96). We estimated body condition as body mass divided by tarsus length. As an index of ectoparasites, we counted the number of holes in the primary, secondary (both wings), and tail feathers made by feather lice (Dunn et al. 1994). We checked nest boxes daily, or every other day, from late April until early July to determine lay date, clutch size, hatching and fledging success. Nestlings were weighed and measured (tarsus and ninth primary length) at 12 days of age. A small blood sample (≤50 ul) was collected from all adults and nestlings and stored in lysis buffer at 4 °C. Unhatched eggs and dead nestlings were collected and tissues were frozen at −20 °C. To directly compare the traits of males that were successful extra-pair sires with the male they cuckolded, we analyzed all broods with mixed paternity, from six breeding seasons (1997–2002), that were not part of any experimental manipulation prior to incubation that could have influenced paternity.

Analysis of Parentage.—Parentage of nestlings was determined using highly polymorphic combinations of microsatellite loci. In this study we analyzed 93 broods of mixed paternity from 1997–2002. We used eight loci in 1997–1999 (n = 32 broods, P_{et} = 0.9996; Whittingham et al. 2006), seven loci in 2000 (n = 29 broods, P_{et} = 0.993; Dunn et al. 2009), and four (P_{et} = 0.996) or eight loci (P_{et} = 0.9996) in 2001 (n = 17 broods) and 2002 (n = 15 broods; Dunn and Whittingham 2007). In 2001 and 2002, four loci were initially used for paternity exclusion, then an additional four loci (eight loci total) were used for assignment of extra-pair sires.

Details of microsatellite amplification, visualization, determination of within-pair and extra-pair young, and assignment of extra-pair sires are given in Whittingham et al. (2006), Dunn and Whittingham (2007), and Dunn et al. (2009).

Nestlings were considered within-pair young if they matched the putative father at all loci and extra-pair young if they mismatched the putative father at two or more loci. There were no cases in

TABLE 1. Male traits (mean ± SD) for extra-pair sires and the within-pair male they cuckolded in Tree Swallows studied in Saukville, Wisconsin, 1997–2002. $P < 0.05$ is indicated in bold and n represents the number of paired comparisons. Effect size (Cohen's d) and confidence interval (CI) are given for each paired test.

	n	Extra-pair sire	Within-pair male	Paired t	P	Cohen's d	CI
Breeding experience (years)	118	0.9 ± 1.1	0.6 ± 0.9	2.15	**0.033**	0.2779	0.0215–0.5343
Body condition	109	1.68 ± 0.12	1.65 ± 0.12	1.93	0.054	0.2448	−0.0216–0.5113
Body mass (g)	120	21.0 ± 1.33	20.6 ± 1.32	2.35	**0.021**	0.2864	0.0320–0.5407
Wing length (mm)	108	121.0 ± 3.23	120.0 ± 3.13	2.49	**0.015**	0.3143	0.0460–0.5827
Tarsus length (mm)	111	12.57 ± 0.46	12.51 ± 0.40	0.91	0.367	0.1386	−0.1248–0.4020
Keel length (mm)	111	22.19 ± 0.78	22.04 ± 0.74	1.44	0.153	0.1965	−0.0672–0.4603
Tail length (mm)	104	58.59 ± 2.32	58.42 ± 1.86	0.57	0.570	0.0808	−0.1911–0.3527
Total feather lice holes	111	9.3 ± 8.7	14.8 ± 21.5	−2.57	**0.012**	0.3359	−0.6009–0.0710

which a nestling mismatched the putative father at only one locus. To assign extra-pair sires, the paternal alleles of the extra-pair young were compared to the alleles of all males sampled in the population. Extra-pair sires were assigned only when one male matched an extra-pair young at all loci. For 93 broods with mixed paternity, we genotyped 92% of all eggs laid (444/485), including embryos of 20 unhatched eggs.

Data Analysis.—We used matched-pairs analysis in JMP Pro 10 (SAS Institute 2012) to compare extra-pair sires with the within-pair male they cuckolded. There were no pairs of within-pair and extra-pair males that were represented in more than one year. In each model, we included brood identity as a grouping variable to take into account the multiple comparisons that occurred when there were multiple extra-pair sires in one brood. In this sample of broods with mixed paternity, there were 27 broods with 2 identified extra-pair sires, 7 broods with 3 identified extra-pair sires, and 1 brood with 4 identified extra-pair sires. In many cases the sire of the extra-pair young could not be identified from the males sampled in the population (see below). Of the 93 broods with mixed paternity, there were 132 comparisons between within-pair and extra-pair males. Broods from 1997 were not included in the analysis of male breeding experience, because our study population was initiated that year and, thus, breeding experience was not known for those birds. Means are presented with their standard errors and all tests are two-tailed. For paired t-tests the standardized effect sizes (Cohen's d) with 95% confidence intervals (CI) were calculated using the 'effect size calculator' (David B. Wilson; www.campbellcollaboration.org/resources/effect_size_input.php). The means and standard deviations option was used in order to not overestimate effect sizes in paired tests (Dunlap et al. 1996).

RESULTS

Of the 93 broods with mixed paternity, 33% (148/444) of young were sired by the social mate (i.e., within-pair young) and 67% (296/444) of young were sired by an extra-pair male. We were able to assign extra-pair sires for 45% (132/296) of the extra-pair young. Thus, the actual sire was known for 63% (280/444) of all young.

In our population of Tree Swallows, successful extra-pair sires were more experienced breeders and had longer wings, greater body mass, and fewer lice holes in their feathers than the within-pair male they cuckolded (Table 1). Body condition also tended to be greater for extra-pair sires (Table 1). However, extra-pair sires and the males they cuckolded did not differ in other indices of body size, including tarsus, keel, or tail length (Table 1). Body mass was positively related to wing length ($r^2 = 0.07$, $P = 0.01$, $n = 94$), but not to tarsus ($r^2 = 0.002$, $P = 0.67$, $n = 96$), keel ($r^2 = 0.03$, $P = 0.1$, $n = 95$), or tail length ($r^2 = 0.001$, $P = 0.7$, $n = 92$).

DISCUSSION

In birds, extra-pair mating can influence the strength of sexual selection, and paired comparisons between within-pair and extra-pair sires provide a powerful way to identify sexually selected traits that influence male fertilization success. Similar to many other species of birds, our study of Tree Swallows revealed that extra-pair fertilization success was correlated with male body size (wing length) and breeding experience, a correlate of age and, hence, survival. However, there also appears to be some variation between

TABLE 2. Studies using paired comparisons of extra-pair sires and the male they cuckolded in multiple populations of the same species. Male characteristics listed as significantly different were greater in the extra-pair sire than the cuckolded male (i.e., body mass) unless stated otherwise (i.e., fewer lice holes).

Species	Study location	Paired comparison		Reference
		Significant differences	Non-significant differences	
Tree Swallow *Tachycineta bicolor*	Wisconsin, USA	breeding experience, body mass wing length fewer lice holes in feathers	tarsus, tail & keel length body condition (P=0.054)	this study
	Ontario, Canada	body mass & condition fewer lice holes in feathers	tarsus & wing length	Kempanears et al. 2001
	British Columbia, Canada	none	plumage hue & chroma, wing length, body mass	Bitton et al. 2007
Common Yellowthroat *Geothlypis trichas*	Wisconsin, USA	mask size, breeding experience	body condition, song rate	Thusius et al. 2001
	Wisconsin, USA	mask size	bib size & color, body mass	Garvin et al. 2006
	New York, USA	none	mask & bib size, yellow chroma, yellow & UV brightness[1]	Freeman-Gallant et al. 2010
Blue Tit *Cyanistes caeruleus*	Corsica, France	none	tarsus & wing length, age, body mass & condition, relatedness to female	Charmantier et al. 2004
	Vienna, Austria	age, tarsus length	none	Foerster et al. 2003
	Vienna, Austria	age	crown color (hue & UV chroma)	Delhey et al. 2007
	Schoten, Belgium	age, tarsus & strophe length, lower body condition	none	Kempenaers et al. 1997
Great Tit *Parus major*	Wuppertal, Germany	none	tarsus & wing length, breast stripe width	Strobach et al. 1998
	Aburayama Nature Reserve, Japan	breast stripe width lower relatedness to female	tarsus length	Kawano et al. 2009
	Arnhem, Netherlands	none	tarsus length, body mass, age, survival, exploratory score	van Oers et al. 2008
Reed Bunting *Emberiza schoeniclus*	Gletterens, Switzerland	none	song rate & diversity, relatedness to female	Suter et al. 2007, 2009
	De Biesbosch National Park, Netherlands	age, wing length	song rate, repertoire size, tarsus length, body mass, badge color & size song characteristics, cloacal protuberance	Bouwman et al. 2007
	Øvre Heimdalen, Norway	none	genetic heterozygosity, relatedness to female	Kleven and Lifjeld 2005

TABLE 2. Continued.

Species	Study location	Paired comparison: Significant differences	Paired comparison: Non significant differences	Reference
House Wren *Troglodytes adeon*	Wisconsin, USA	none	breeding experience, body condition, survival	Poirier et al. 2004
	Wyoming, USA	rare alleles	heterozygosity relatedness to female	Masters et al. 2003
Pied Flycatcher *Ficedula hypoleuca*	Turku, Finland	none	tarsus length, dorsal coloration, UV reflectance, forehead patch size	Lehtonen et al. 2009
	Sevilla, Spain	tarsus length, forehead patch size, darker dorsal coloration	wing length, wing patch size, body mass, age	Canal et al. 2011
America Redstart *Setophaga ruticilla*	Pennsylvania, USA	none	carotenoid coloration, tarsus & wing length, body mass	Kappes et al. 2009
	Ontario, Canada	flank & tail redness	body & bib size	Reudink et al. 2009
Red-winged Blackbird *Agelaius phoeniceus*	Ontario, Canada	age, lifespan	body & epaulet size	Weatherhead and Boag 1995
	Kentucky, USA	none	body & epaulet size, extent of non-black plumage	Westneat 2006

[1] Examined only among males that were experienced breeders.

populations of Tree Swallows in traits associated with extra-pair mating. Below we review some of these differences and present some hypotheses and recommendations for future studies which may also help to reconcile differences between studies in other species of birds.

Our results are similar to a previous study of Tree Swallows breeding in Ontario (ON, Kempenaers et al. 2001) but not to a study conducted in British Columbia (BC; Bitton et al. 2007; Table 2). Extra-pair sires in both Wisconsin (WI) and ON were heavier and had fewer lice holes in feathers than the male they cuckolded. These may be important signals of male quality, as lice holes in feathers reduce the fitness of aerial insectivores (Barbosa et al. 2002), and heavier males in better condition are more likely to acquire a nest box (Lozano 1994). Heavier males may also be better able to circumvent mate guarding by the female's social mate. This might be important in other species of birds; however, male Tree Swallows do not actively guard their mates (Leffelaar and Robertson 1984), but instead, attempt to assure their paternity through frequent copulations (Venier and Robertson 1991).

Extra-pair mating appears to produce comparable selection on body mass and feather parasitism of Tree Swallows in ON and WI. In WI extra-pair sires also were more experienced breeders (0.3 years mean difference, n = 118 pairs, range 0–5 years), which may signal male quality to females because it reflects survival, and older males arrive earlier at breeding sites (Robertson et al. 1992). Breeding experience was not reported for ON or BC. Male wing length was measured in all three populations and in WI extra-pair males had longer wings than the cuckolded male (1.0 mm mean difference, n = 108 pairs), but not in ON (0.1 mm difference, n = 11 pairs) or BC (0.05 mm difference, n = 14 pairs). On the other hand, another measure of size, tarsus length was not associated with extra-pair fertilization success in either ON (0.37 mm difference, n = 9 pairs) or WI (0.06 mm difference, n = 111 pairs; not measured in BC), so these discrepancies may not simply occur because of sample size differences. A more interesting possibility is that there is countervailing selection against larger males as a consequence of aerial foraging or the need to fit inside small cavities for nesting and the intensity of that selection varies between populations. Consistent with this hypothesis, we found that wing (coefficient of variation, CV = 2.7%) and tarsus (CV = 3.6%) length were less variable than body mass (CV = 6.3%), feather holes from lice (CV = 136%) and breeding experience (CV = 132%). If fertilization success is based on female choice of male traits, then the greater variation in male body mass and feather holes may be more informative about male quality.

In Tree Swallows, older experienced males have brighter dorsal plumage than younger inexperienced males, which may also be an indicator of male quality (Bitton and Dawson 2008). Consistent with this idea, extra-pair mating success in BC was correlated positively with male plumage brightness (not measured in ON or WI) in a population wide comparison, but there was no difference in plumage brightness, body mass, or wing length in paired comparisons between extra-pair sires and the male they cuckolded (Bitton et al. 2007). The lack of selection on body mass (and presumably condition) and wing length in BC could be related to ecological and behavioral differences between BC and the two eastern study sites, such as variation in the availability of nest sites. Nest box occupancy was only 50% in BC, compared to 98% in both WI and ON, although nest-box spacing was similar in all three populations (27–40 m apart in WI and ON, 20–30 m apart in BC). Male Tree Swallows are under strong selection to acquire a nest box each spring, which favors early arrival dates and males in better condition (Lozano 1994). Thus, selection on body mass and condition may be stronger in populations where breeding opportunities are limited and competition is more intense (WI and ON), compared to populations where vacant nest sites are abundant and competition less intense (BC).

The differences between populations in nest box occupancy will also result in differences in breeding density, which may influence the frequency of extra-pair mating and, thus, selection on male traits. While the overall proportion of broods containing extra-pair young was similar among these three populations of Tree Swallows, the percentage of extra-pair young in the population was lower in BC, and fewer broods had more than one extra-pair sire in BC than in WI or ON (Table 3). This suggests that selection through extra-pair fertilizations may not be as strong in BC. Although both breeding density and synchrony have been associated with variation in the level of extra-pair mating for many species of birds (e.g., Stewart et al. 2010, Canal et al. 2012; but

TABLE 3. The level of extra-pair mating in three populations of Tree Swallows breeding in Wisconsin (Dunn et al. 2009), Ontario (Kempenaers et al. 2001), and British Columbia (Bitton et al. 2007), given as the percentage of broods with extra-pair young (EPY), percentage of broods with more than one extra-pair sire (EPS), the percentage of EPY in the population, and the percentage of EPY assigned to extra-pair sires. Samples sizes (*n*) are number of broods sampled/number of nestlings genotyped.

Study site	% Broods w/EPY	% Broods >1 EPS	% EPY	%EPY assigned	*n*
Wisconsin	83	51	49	45	41/206
Ontario	76	62	52	65	21/117
British Columbia	85	36	35	42	40/216

see Dunn et al. 1994), to our knowledge no one has related differences between populations in breeding density or synchrony to differences in sexual selection on male traits.

In other species of birds, comparisons of multiple populations seem to show differences more often than similarities in male traits associated with extra-pair fertilization success. However, there are surprisingly few examples using paired comparisons of traits between extra-pair sires and the male they cuckolded (Table 2). In Eurasian Blue Tits (*Cyanistes caeruleus*), male body size (tarsus length) was related to male survival (Kempenaers et al. 1997) and extra-pair sires were larger (longer tarsus) and older than the male they cuckolded in populations studied in Belgium and Austria (Kempenaers et al. 1997, Foerster et al. 2003, Dehley et al. 2007), but not in a population studied in Corsica (Charmantier et al. 2004; Table 2). Perhaps, like Tree Swallows, these traits may differ between populations in how they reflect male quality because of environmental differences between sites.

Extra-pair mating can also lead to sexual selection on ornamental plumage traits (Table 2). For example, in Great Tits (*Parus major*), size of the male breast stripe reflects ability to cope with oxidative stress (studied in Spain, Galván and Alonso-Alvarez 2008, 2010), supporting the idea that breast stripe size is an indicator of male quality (Norris 1990). As expected, extra-pair sires had larger breast stripes than the male they cuckolded in a population studied in Japan (Kawano et al. 2009), but not in Germany (Strohbach et al. 1998), suggesting that the reliability of the breast stripe as an indicator of male quality may differ between populations. This may be the case for other species of birds as well. There are several other species for which researchers have used paired comparisons and identified a trait(s) associated with success as an extra-pair sire in one population but not in another population (Table 2).

Differences between populations in sexually selected traits may arise because signals become less reliable as indicators of male quality as selective environments change (Schluter and Price 1993, Vergara et al. 2012) or female preferences switch from one trait to another (e.g., Chaine and Lyon 2008). These hypotheses predict that such ornaments should be less variable in the population where they are no longer sexually selected. It should be easy to test predictions about the variability of traits between populations, but the necessary information is often not published. In future studies, it would be valuable to include data on the variation in male traits, as it would facilitate comparisons between populations and meta-analyses of geographic variation in sexual selection. Comparisons between populations in traits associated with extra-pair fertilization success are difficult if researchers do not measure the same traits (see Table 2) and if the traits associated with extra-pair and within-pair fertilization success differ. For example, Barn Swallows (*Hirundo rustica erythrogaster*) in North America have two age-dependent sexually selected traits: tail streamer length and ventral plumage coloration (Lifjeld et al. 2011). A population studied in Ontario, Canada found that tail streamer length (but not ventral coloration) correlated positively with extra-pair fertilization success (paired analysis; Kleven et al. 2006), whereas in a New York population, darker ventral coloration correlated positively with higher within-pair paternity (Safran et al. 2005). However, comparisons between these two populations are difficult because male fertilization success was not measured the same way in both studies. A more recent study in Virginia (Eikenaar et al.

2011) assigned sires to extra-pair young and found that darker ventral coloration was correlated with within-pair but not extra-pair fertilization success (Eikenaar et al. 2011) suggesting that Barn Swallows may be an example of a species with one trait (tail streamer length) selected through extra-pair success and a different trait (ventral coloration) selected through within-pair fertilization success.

Both paired comparisons and population wide analyses attempt to identify male traits selected through extra-pair mating success. When population sampling is relatively complete and most or all of the extra-pair sires can be identified, then both types of analyses are likely to reveal the same traits (Thusius et al. 2001, Kleven et al. 2006). However, when it is not possible to assign paternity to many of the young, the results of paired comparisons and population wide analyses may differ (Kempenaers et al. 2001, Bitton et al. 2007, Bouwman et al. 2007, Canal et al. 2011). These differences may be particularly important if the unassigned young are sired by males that are not random with respect to the sexually selected trait (Sardell et al. 2010). Indeed, if specific male traits are associated with success as an extra-pair sire, then it is unlikely that unassigned males are truly random with respect to these traits. Thus, paired comparisons of extra-pair sires and the male they cuckolded may be less biased because both the within-pair and extra-pair males are sampled. Furthermore, paired comparisons help to control for variation in the quality of within-pair mates. For example, females may be less likely to engage in extra-pair mating if they are paired to a high quality male who is more attractive or better able to protect his within-pair paternity. Finally, a greater effort should be made in the future to conduct studies that are comparable between populations (i.e., measuring the same male traits, reporting variance, and distinguishing between traits associated with extra-pair versus within-pair success). In addition, accounting for habitat differences between populations, or studying populations that breed in different habitats, will lead to a better understanding of how environmental heterogeneity influences selection on male traits.

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BIRD MORTALITY DURING NOCTURNAL MIGRATION OVER LAKE MICHIGAN: A CASE STUDY

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ABSTRACT.—Millions of birds die each year during migration. Most of this mortality goes unobserved and conditions surrounding the actual events are often not thoroughly documented. We present a case study of substantial migrant casualties along the shores of southwestern Lake Michigan during May 1996 when we found 2,981 dead birds of 114 species, mostly migrant passerines. An unusual sequence of events allowed us to document the circumstances surrounding this migratory bird kill. Bird carcasses appeared on the southwestern shores of Lake Michigan in the days following storm systems that produced high rain and in one case, hail. Encounters between birds and precipitation over open water were recorded by weather radar, and were followed by winds that drifted dead birds toward highly populated shorelines where the kill was observed and documented. Climatologically, May 1996 was exceptional for producing weather conditions that both killed birds *en masse* and allowed the mortality to be documented. As a result, this is one of the more thoroughly documented instances of a weather-related mass mortality event during migration. *Received 14 December 2012. Accepted 2 September 2013.*

Key words: migration, mortality, open water, weather, weather radar.

Migration is likely the most hazardous phase of the avian life cycle for many species of birds (Sillett and Holmes 2002, Paxton et al. 2007). Despite persistent concern and debate about the health of North American migratory bird populations (Newton 2004, Faaborg et al. 2010), avian mortality during migration remains poorly understood. Anthropogenic sources of mortality during migration have received much recent scrutiny (Kunz et al. 2007, Gehring et al. 2011), but their toll on bird populations is not well known, and even greater uncertainty surrounds the impacts of natural hazards that birds face during migration. In the western hemisphere many species cross long stretches of open water in biannual migrations (Gauthreaux 1971, McClintock et al. 1978, Russell 2005), and during particularly stormy seasons, mortality associated with open water crossing may account for measurable population declines in some North American bird species (Butler 2000). A sparse literature documents incidents of bird mortality resulting from encounters with unfavorable weather over water (Newton 2008).

The Great Lakes, which migrants cross in large numbers (Diehl et al. 2003), are essentially inland seas and a documented hazard for migrants. Along the southern shores of Lake Michigan, Deane (1914) cited a May 1888 account of bird mortality in the hundreds between Chicago, Illinois and Milwaukee, Wisconsin. Saunders (1907) reported 1,485 birds found dead on the southern shores of Lake Huron. Segal (1960) reported over 3,600 birds washed up on beaches in Indiana during April 1960. In each of these cases, the authors suggest the total mortality exceeded what they actually found. Other more anecdotal accounts report mortality estimated in the hundreds of thousands along southern Lake Huron (Janssen 1976) and Lake Michigan (Henderson 1927). By comparison, Segal's (1960) relatively thorough collection efforts demonstrated how spotty the shoreline distribution of dead birds can be, complicating attempts to estimate totals from limited sampling. In most of these incidents, the authors attribute bird mortality to encounters with adverse weather such as strong winds or snow over open water (Saunders 1907, Henderson 1927, Segal 1960). However, without more direct information on the circumstances birds face over water, our understanding of this kind of mortality will remain vague.

We report on migratory bird mortality in the thousands documented along the beaches of southern Lake Michigan during mid- and late-May 1996. We describe this mortality in terms of natural history and determine whether it could be attributed to birds encountering unfavorable weather by, 1) using archived data from weather radar to document instances when birds encountered unfavorable weather over Lake Michigan, and 2) examining how changes in species composition and the physical properties of bird

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carcasses collected throughout May 1996 correspond with the passage of weather systems. We also consider the mechanisms by which weather may lead to such mortality and why these events have not been documented more frequently on the Great Lakes.

METHODS

We first discovered bird carcasses washing up on a beach of Lake Michigan in northern Chicago, Illinois on 11 May 1996. Following the initial discovery, personnel of the Field Museum of Natural History's Bird Division began surveying and collecting dead birds on additional beaches in the Chicago area. Six beaches with a combined length of approximately 2 km were surveyed on 12 days between 11 May and 1 June. In addition, one long stretch of beach at Illinois Beach State Park north of the city was surveyed on 29 May.

We brought birds or parts of birds to the museum and identified them to species. Most were preserved as skeletons and catalogued into the collections of the Field Museum. We attempted to classify all individuals to sex by examination of gonads at time of preparation. We assigned subcutaneous fat scores when possible to one of six categories (none, trace, light, moderate, heavy, extreme) following standard procedures. Specimens were discarded if their condition prevented us from determining sex or assigning a fat score.

We examined day-to-day changes in species' relative abundance on the premise that daily collections of beached birds would exhibit greater similarity in species abundance if associated with the same causal event. Relative abundance was determined for all species represented by ≥50 individuals across the entire collection. Thirteen species met this criterion (see Appendix) and accounted for 72% of all birds collected. Day-to-day relative abundances among these species varied considerably among collections large enough to include in this analysis (11, 12, 17, 27, 29, and 31 May), so rank correlations were used to compare species' relative abundances between all pairs of collection days for the 13 most abundant species.

The proportion of carcasses discarded was evaluated descriptively for changes consistent with one or multiple events. If all mortality was the result of a single early event, the proportion discarded would increase as time passed owing to continuing decomposition. Conversely, overall mortality is more likely explained by multiple events if the proportion discarded decreases or remains relatively unchanged through time. Also, we examined species sex ratios descriptively and used regression to examine how abundances of the most common species in the kill varied with fat score.

Archived data from local Doppler weather radar (National Weather Service station KLOT in Romeoville, IL, 47 km WSW of Lake Michigan) was used to identify encounters between birds and precipitation over water and synchronize those events with collections of beached birds. Level II radar data (Crum et al. 1993, Diehl and Larkin 2005) covering southern Lake Michigan were obtained for this radar from the National Climate Data Center (NCDC; NOAA 2012a) for May 1996. These data were analyzed using WATADS version 10.2 (NOAA 2000). We examined radar reflectivity factor (hereafter, reflectivity), radial velocity, and spectrum width data from Doppler radar for all instances where birds likely encountered precipitation over southern Lake Michigan during May 1996. Reflectivity provides a measure of the amount of transmitted radio energy that targets reflect back to the radar (i.e., radar echo). Radial velocity indicates the speed and direction of targets relative to the radar. Spectrum width offers a measure of the variation in target velocities. For a more complete description of this weather radar system's biological capabilities, see Diehl and Larkin (2005), Chilson et al. (2012), and Larkin and Diehl (2012).

We examined target airspeeds to ensure that migrations were dominated by birds and not arthropods (Larkin 1991, Gauthreaux and Belser 1998, Diehl et al. 2003, Gauthreaux et al. 2003). Radiosonde data were not available from the Chicago area National Weather Service station (KLOT). However, synoptic maps showing interpolated winds from nearby stations allowed us to choose radiosonde data from nearby stations experiencing winds that most closely matched those in northwest Illinois, specifically, from Lincoln, Illinois (KILX); Davenport, Iowa (KDVN); and White Lake, Michigan (KDTX).

We determined whether northeasterly winds produced currents that carried dead birds toward shores in Chicago by evaluating mean daily winds recorded at a weather buoy in southern Lake Michigan (buoy 45007 at 42° 40′ 11″ N, 87° 1′ 12″ W; NOAA 2012b). These were examined against trends in numbers of birds collected and radar indications of birds encountering precipitation over

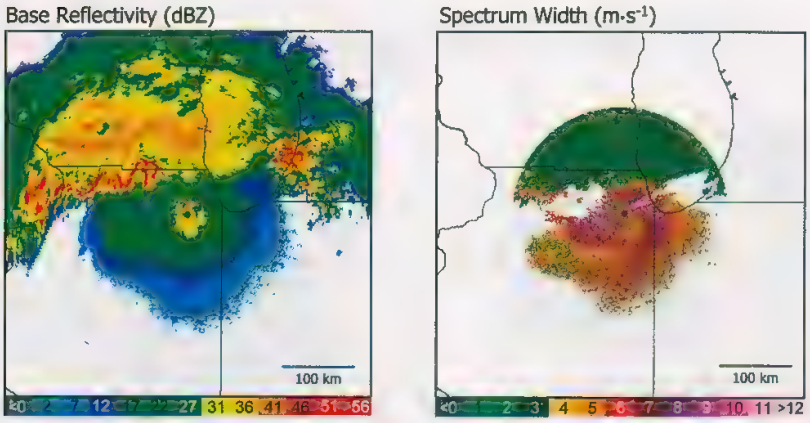

FIG. 1. Base reflectivity and spectrum width of birds and precipitation on 10 May 1996 at 0100 CST (Central Standard Time). (Left) Radar reflectivity showing precipitation stretching across the entire image to the north of a semi-circular, concentric pattern of bird echoes. The black dot marks the location of the radar (KLOT) in Romeoville, Illinois. (Right) Precipitation and birds differ markedly in the corresponding spectrum width image. White voids in the pattern show regions where spectrum width measures proved unreliable. Spectrum widths beyond 148 km range from the radar are not shown, because velocity-based metrics (including spectrum width) is unambiguously calculated only out to certain ranges.

water. We also determined whether or not May 1996 was exceptional in a broader context by examining the amount of precipitation (as an indication of unfavorable weather, recorded Chicago Midway International Airport) and the propensity for northeasterly winds (at buoy 45007 in southern Lake Michigan) during the month of May each year from 1991–2012.

RESULTS

We collected 2,981 dead birds representing 114 species from shores in the Chicago area in 12 days throughout May (see Appendix) with largest numbers on 11, 12, 17, 27, 29, and 31 May. The single most speciose day, 29 May, yielded 1,149 individuals from 87 species. Fat score and sex could be determined for 75.0% and 59.6% of individuals respectively. In 14.7% of cases, fat score or sex could not be determined, and these carcasses were discarded. We cannot reliably estimate total mortality, although salvaged birds likely represented a small fraction. We saw many birds floating in the water where they could not be recovered. Many probably sank or were scavenged by fish, gulls, and crows (Ebener 1997; DEW, pers. obs.). The sample was dominated by sparrows (Emberizidae; 39.24%, n = 1,170) with White-throated Sparrows (*Zonotrichia albicollis*) and Swamp Sparrows (*Melospiza georgiana*) being most abundant (31.6%, n = 943). Warblers (Parulidae) were the next most abundant family (30.42%, n = 907), but their numbers were not concentrated in a few species.

The female to male sex ratios and amount of subcutaneous fat varied among species. The sex ratio of sparrows strongly favored females (f:m sex ratio = 3.63) and explains in large measure the female bias in overall sex ratio among specimens where sex could be determined (f:m = 1.52, n = 1,764). In contrast to sparrows, warblers exhibited a male-biased sex ratio (f:m = 0.76) and showed 'trace' median subcutaneous fat. The median subcutaneous fat score for Emberizids was 'heavy.' Among the 12 most abundant species, abundance increased as function of mean fat score (r^2_{adj} = 0.32, P = 0.033). Prior to testing, abundance measures were log transformed to adjust for heteroscedasticity in the data.

We identified radar targets attributable to birds and precipitation prior to assessing interactions between the two over open water. All migrations showed biological echoes having airspeeds consistent with bird-dominated migration (12.43 ± 3.66 m/sec). In this study, spectrum width, and to some degree reflectivity, were the most useful of the three base data types in discriminating birds from precipitation, especially when echoes caused by birds and precipitation were in close proximity over water. Radar echoes dominated by precipitation exhibited lower spectrum widths than echoes dominated by birds (Fig. 1; see also Larkin and Diehl 2002). Echoes attributed to birds also appeared over land shortly after local evening twilight, consistent with known departure times for migrants (Cochran et al. 1967, Hebrard

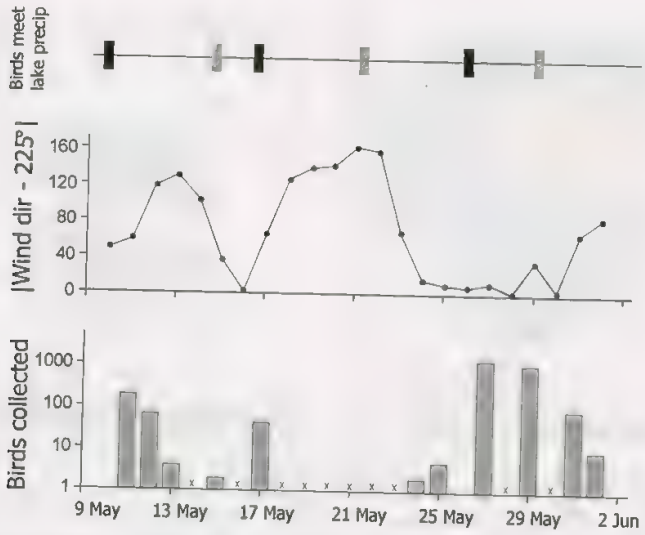

FIG. 2. Timing of bird carcasses collected along the shores of Lake Michigan in Illinois and precipitation events followed by favorable on-shore winds during May 1996. (Top) Bars along the top mark events where radar shows migrating birds encountered precipitation over Lake Michigan. Black bars indicate likely stronger encounters. (Middle) Absolute value of wind direction measured from a weather buoy in lower central Lake Michigan minus the direction toward Chicago's coastline (225). Absolute value differences are lowest when winds are toward the shores of Chicago. (Bottom) Numbers, shown in log scale, of dead birds collected along area beaches in Chicago. 'X' indicates days when shores could not be surveyed.

1971), exhibited reflectivity consistent with those reported for migrating birds (Gauthreaux and Belser 1998, 1999; Dokter et al. 2010), did not exhibit reflectivity usually associated with strong precipitation (Rinehart 1997), decreased in reflectivity with range (Diehl and Larkin 2005, Buler and Diehl 2009), and were characteristically absent at long ranges under standard refraction (Fig. 1; Base Reflectivity) and on higher elevation sweeps of the radar's beam. Spectrum widths also were more consistent with migrating birds than arthropods (Larkin and Diehl 2002), and the more homogenous radial velocity fields characteristic of arthropod-dominated migrations were absent (Dokter et al. 2010).

The timing and intensity of encounters between birds and precipitation over water corresponded with distinct mortality events identified from species abundance data. Examination of reflectivity and spectrum width data for May 1996 revealed six instances of birds likely encountering precipitation over water between 9 May–1 June. Storm systems associated with these encounters all occurred over the southern end of Lake Michigan after the onset of nocturnal migration. Three nocturnal encounters, 9–10, 16–17, and 25–26 May, showed prominent mixing of birds and precipitation over water (Fig. 2) that preceded taxonomically distinct collections of beached birds. Storm and migrant activity on the night of 9–10 May illustrate such an encounter (Fig. 3). In this instance, velocities and storm cell tracks measured using radar indicated widespread rainfall moving toward the ENE at >25 m/s. Migrating birds encountered a particularly strong band of precipitation (up to and occasionally exceeding 60 dBZ) over the southern end of Lake Michigan. A vertical cross section of these echoes shows precipitation extending higher than 10 km above ground level, towering over the much lower migratory bird layer.

The amount and kinds of precipitation, and the propensity for northeasterly winds along shores of northeastern Illinois likely relate to both the cause and documentation of this mortality respectively. Climatologically, May 1996 experienced the greatest propensity for northeasterly winds and among the highest levels of precipitation compared to May of other years from 1991–2012 (Fig. 4).

Weather radar data suggest that the mortality documented during May 1996 occurred as a result of multiple weather-related events. Changes in the relative abundance of species and the conditions of bird carcasses offer further evidence that the mortality resulted from at least two separate

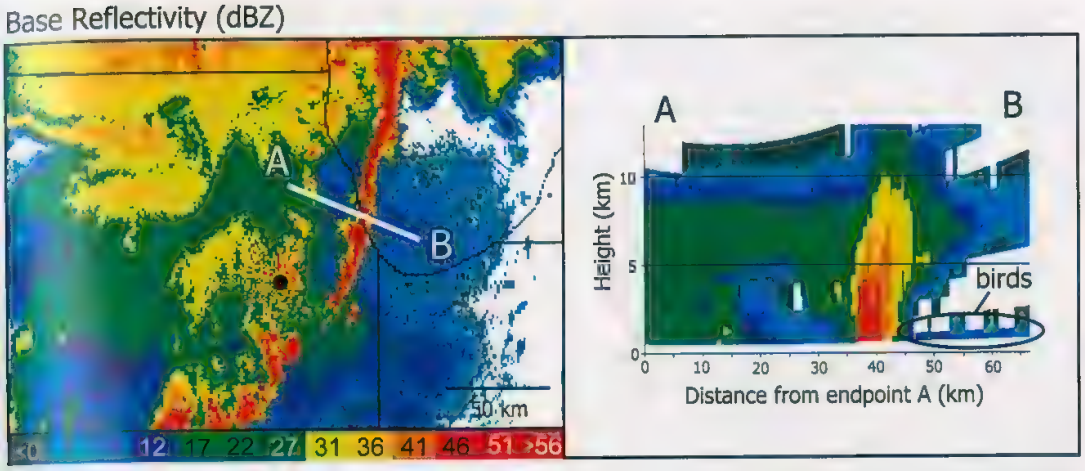

FIG. 3. Reflectivity of precipitation and migrating birds (left) around southern Lake Michigan at 0322 CST (Central Standard Time), 10 May 1996. The black dot marks the location of the radar. Reflectivities of birds varied around 12 dBZ (blues), while stronger precipitation echoes tend to exceed 17 dBZ (greens, yellows, reds). Segment AB (left) shown in cross-section (right) passes through a region of radar echo where birds meet strong precipitation over water. The band of precipitation visible in the left image is clearly seen as a towering region of high reflectivity.

events, those during the nights of 9–10 May and 25–26 May.

The correlation matrix of rank relative species abundances between pairs of collection days shows that collection days were only correlated significantly when near in time and coincident with the same weather event (Table 1). The proportion of birds discarded because of condition was lowest for birds collected on the first day following a prominent interaction between birds and weather over water and increased on subsequent days; specifically, 0.14 to 0.17 discarded from 11 and 12 May respectively, 0.03 to 0.17 discarded from 27 to 31 May respectively.

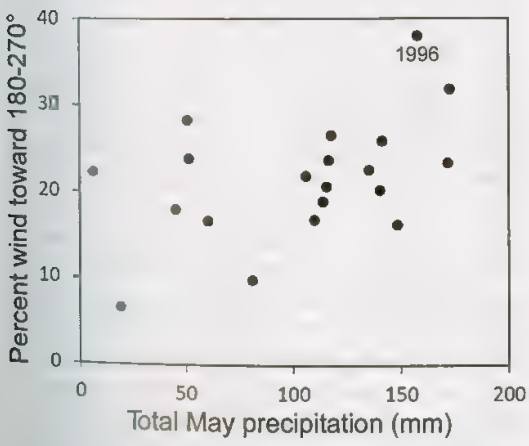

FIG. 4. May 1996 exhibited an exceptional proportion of winds toward the coastline of the Chicago area and high amounts of precipitation compared to other Mays during the 1990s and 2000s. (Wind direction data from May 1999 and May 2000 were missing.)

DISCUSSION

Historic data from weather radar and water- and land-based weather stations enabled us to reconstruct the circumstances leading to considerable bird mortality documented along the shores of Lake Michigan in northeastern Illinois. These data, supported by our data from carcasses we collected along shorelines, suggest that birds died in encounters with at least two storm systems while migrating over southern Lake Michigan during May 1996. Storm activity the night of 9–10 May, followed by winds from the northeast, preceded arrival of bird carcasses on northeastern Illinois shores during 11–12 May. Birds collected on 17 May either died in encounters with the storm activity of 16–17 May or 9–10 May (the latter likely failed to beach for several days [e.g., Bibby and Lloyd 1977] until the return of northeast winds on 15 May). Despite winds from the northeast for 2 days preceding storm activity on 25–26 May, few birds were collected until after the storm's passage, suggesting the collections from 27–31 May represented mortality associated with storms of 25–26 May. Our estimations of species' relative abundances derived from the birds collected were statistically similar in the days immediately following storms

TABLE 1. Correlation matrix showing similarity in relative abundance of species between days when the majority of bird carcasses were collected. Spearman's rank correlation (r_s) and P-values (in parentheses) are given for each day-by-day comparison. Significant correlations are bold.

	11 May	12 May	17 May	27 May	29 May
12 May	**0.78** (**< 0.002**)				
17 May	−0.16 (0.59)	−0.03 (0.92)			
27 May	0.05 (0.88)	0.04 (0.90)	0.50 (0.085)		
29 May	0.07 (0.81)	−0.01 (0.98)	0.27 (0.38)	**0.69** (**< 0.009**)	
31 May	0.14 (0.66)	0.17 (0.58)	0.29 (0.33)	**0.68** (**< 0.011**)	**0.86** (**< 0.001**)

and statistically different when comparing collections between storms.

It is highly improbable that birds collected on 27–31 May died during a storm before 25–26 May. This would require that birds remain afloat for 10–16 days; that birds beach roughly *en masse* (few birds were collected in the days preceding the large 27 May collection) after riding varied currents for more than a week; and that the carcasses survive largely intact after many days of drifting without sinking or being taken by airborne or aquatic scavengers. The proportion of corpses discarded owing to condition was lowest for the first collection following storms (i.e., 11, 17, 27 May). This proportion increased in subsequent days (i.e., 12 May and 29, 31 May; no collections followed 17 May) which would be expected for corpses that experienced greater exposure to the elements and scavengers.

The conditions that caused the bird kills of May 1996 and resulted in their documentation rely on a chain of events that likely occurs infrequently with respect to any one shoreline. The mortality occurred on nights when migratory birds had flown over the lake before the appearance of storm activity. The encounter between birds and severe weather over the lake killed birds, and the total mortality was likely much greater than what we recorded. Winds following these encounters pushed bird carcasses toward the shore in large numbers, but most may have sunk or been scavenged. Whether or not carcasses reach shore is probably a complicated function which includes how long birds stay afloat (which varies by species, Simons 1985); the persistence, direction, and strength of prevailing winds and currents; and proximity of the mortality to land (Bibby and Lloyd 1977). Finally, because winds directed the kill toward a shoreline with a dense human population, the event had a high probability of being recognized and documented.

Previous reports of bird kill events associated with migration over water speculate on specific causes of mortality (Saunders 1907, Henderson 1927, Segal 1960, Wiedenfeld and Wiedenfeld 1995; see Newton 2008), but exactly how weather kills migrating birds remains poorly understood because these events are difficult to detect with the aid of technology, let alone observe directly. Storms that produce extremely high rain rates or hail may physically drive down birds. Heavy precipitation and hail occurred during storm activity on 9–10 May. We estimate that a 50 dBZ storm could drop the equivalent of a small bird's mass (e.g., 15 g) on its body nearly every 5 mins. Flying birds drenched by water may become too saturated to produce adequate lift, experience increased wing-loading, or simply drop under continuous pounding. Birds attempting flight with high wing loads, or in strong downdrafts (Rate 1957, Wilson and Wakimoto 2001), or with prolonged exposure to headwinds may succumb to exhausted fat reserves or lactic acid accumulation, lose lift, and drop (although dropping into the water is not certain death for a landbird; McClintock et al. 1978, Brock 1986). Levels of subcutaneous fat in the birds we examined averaged at the high end of our fat scale, suggesting that most did not die because of depleted energy stores. However, birds heavy with fat have increased wing-loading (Lind et al. 1999) and are likely more vulnerable in conditions that exacerbate wing-loading. This latter possibility was supported by a positive relationship between

abundance of dead birds and fat score. Radar-based estimates of rain rate become unreliable when reflectivity is high (Baeck and Smith 1998). Rain rate estimates on WSR-88D increase with reflectivity up to 53 dBZ (Fulton et al. 1998). Precipitation above this reflectivity threshold is likely to include hail which biases rain rate estimates. The leading edge of storm activity on 9–10 May exhibited reflectivities ≥60 dBZ. Reflectivity of this magnitude is typically associated with hail (Balakrishnan and Zrnić 1990; T. Schuur, pers. comm.), otherwise only extremely high rain rates characteristic of more southerly climates cause this much radar echo. Mortality of birds during migration has been associated with hail (Gates 1933, Wiedenfeld and Wiedenfeld 1995), although the paucity of literature documenting such encounters suggest either these events, or the circumstances which allow for their documentation, are uncommon. The continuous operation of large weather radar networks and the ability to interpret their data offer the opportunity to capture rare or unpredictable events and improve our understanding of mortality during migration.

Using radar to identify circumstances when birds encountered precipitation over open water was critical to understanding observed mortality. In this study, radar spectrum width, and to a lesser extent reflectivity, proved useful in distinguishing birds from precipitation in close proximity over water. Precipitation and flying animals generate overlapping distributions of reflectivity, radial velocity, and spectrum width, so the usefulness of any particular combination of variables in discriminating among radar echoes may be case specific. Nonetheless, recently developed algorithms designed to automate this process of target discrimination show promise (Dokter et al. 2010). Advances in radar hardware and signal processing have increased the number of radar variables from the original three base data types mentioned here to include three so-called polarimetric variables (Zrnic and Ryzhkov 1999). This larger parameter space will improve the performance of target classification algorithms moving forward (Park et al. 2009, Dokter et al. 2010), but studies that depend on historic radar data will benefit from capable classification algorithms that rely on the original three variable base data (e.g., Dokter et al. 2010).

Large kills of migrants in the Great Lakes either have occurred infrequently or occur frequently but are seldom documented and reported (Saunders 1907, Deane 1914, Henderson 1927, Segal 1960, Janssen 1976). May 1996 for this region, compared to other Mays between 1991–2012, saw the highest recorded proportion of northeasterly winds and the third highest recorded amount of precipitation. The 25–26 May storm system associated with most of our documented mortality is likely the same system responsible for avian mortality reported among resident birds in southwestern Nebraska (Brown and Brown 1998). This weather event was notable for its duration, cold, and amount of precipitation when compared to records going back to 1875. This suggests the meteorological conditions over southern Lake Michigan that produce substantial mortality along any one shoreline may occur infrequently. However, encounters between birds and precipitation similar to what we monitored likely occur regularly across the Great Lakes. Events that presumably kill fewer birds than the 25–26 May storm (e.g., 9–10 May) might be somewhat common but go unnoticed if carcasses do not remain sufficiently buoyant to become beached or wash up on less populated beaches.

Bias in sex ratios varied by species but favored females overall. Small departures from even sex ratios may result from chance mixing of sexes within the species, but the more extreme examples (e.g., sparrows) likely have non-random drivers. Differential migration, in combination with differences in migration phenology, could produce more extreme sex ratios and explain some of the variation in sex ratio between species. If wing-loading was a factor in this mortality, sex differences in wing-loading may favor one or the other sex depending on species. For example, males exhibit lower wing-loading in some Emberizid species (e.g., Chandler and Mulvihill 1992) which is consistent with our observation that sex ratios of dead birds were highly skewed toward females among the sparrows.

The unplanned 'sampling' associated with beached bird events or birds striking tall anthropogenic structures (e.g., buildings, communications towers, wind turbines) offers chance opportunities to measure the composition of animals flying at night. Species specific behavioral responses to lakes may vary when encountering poor flying conditions over water or engaging in trans- versus circum-lake movements. Most existing methods for monitoring the behavior of these animals offer poor taxonomic resolution (e.g., radar, thermal imaging). Monitored flight

calls of migrating birds have shown promise as a means of measuring species composition aloft, but not all species call during migratory flight; calls within some taxonomic groups cannot yet be classified to species, and many birds fly beyond microphone range (Evans and Rosenberg 1999, Farnsworth 2005). Our sample included species that are largely non-migratory (e.g., Red-bellied Woodpecker [*Melanerpes carolinus*], Northern Cardinal, [*Cardinalis cardinalis*]), species that are usually considered diurnal migrants (e.g., Red-headed Woodpecker [*Melanerpes erythrocephalus*], Blue Jay [*Cyanocitta cristata*]), and species whose migration through Illinois is considered to be completed by early May (e.g., Winter Wren [*Troglodytes hiemalis*], Red-winged Blackbird [*Agelaius phoeniceus*]). Also, there were species (e.g., House Wren [*Troglodytes aedon*]; and vireos) that occurred in much higher proportions of the total kill than in samples of on-shore building kills from Chicago that we have monitored over the last 34 years (DEW, unpubl. data). Documenting the migrating birds killed during these events provides an opportunity, albeit an unpredictable one, to further understand the effects of and behavioral responses to such obstacles.

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APPENDIX. Birds collected (species, numbers) on the southwestern shores of Lake Michigan in Spring 1996.

White-throated Sparrow (*Zonotrichia albicollis*)	497
Swamp Sparrow (*Melospiza georgiana*)	446
Common Yellowthroat (*Geothlypis trichas*)	214
Empidonax (*Empidonax* spp.)	184
Ovenbird (*Seiurus aurocapilla*)	143
Gray Catbird (*Dumetella carolinensis*)	127
Lincoln's Sparrow (*Melospiza lincolnii*)	124
House Wren (*Troglodytes aedon*)	102
Nashville Warbler (*Oreothlypis ruficapilla*)	79
Yellow-rumped Warbler (*Setophaga coronata*)	70
Ruby-crowned Kinglet (*Regulus calendula*)	64
Magnolia Warbler (*Setophaga magnolia*)	60
Palm Warbler (*Setophaga palmarum*)	51
Yellow Warbler (*Setophaga petechia*)	49
Baltimore Oriole (*Icterus galbula*)	38
Chipping Sparrow (*Spizella passerina*)	37
Red-eyed Vireo (*Vireo olivaceus*)	33
Black-and-white Warbler (*Mniotilta varia*)	31
Canada Warbler (*Cardellina canadensis*)	30
Mourning Warbler (*Geothlypis philadelphia*)	27
Sedge Wren (*Cistothorus platensis*)	25
Black-throated Green Warbler (*Setophaga virens*)	25
White-crowned Sparrow (*Zonotrichia leucophrys*)	25
Wilson's Warbler (*Cardellina pusilla*)	22
Swainson's Thrush (*Catharus ustulatus*)	21
Chestnut-sided Warbler (*Setophaga pensylvanica*)	21
Blue-headed Vireo (*Vireo solitarius*)	20
Marsh Wren (*Cistothorus palustris*)	20
American Redstart (*Setophaga ruticilla*)	18
Red-breasted Nuthatch (*Sitta canadensis*)	17
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	17
American Goldfinch (*Spinus tristis*)	16
Yellow-bellied Flycatcher (*Empidonax flaviventris*)	15
Warbling Vireo (*Vireo gilvus*)	15
Northern Waterthrush (*Parkesia noveboracensis*)	15
Yellow-throated Vireo (*Vireo flavifrons*)	14
Savannah Sparrow (*Passerculus sandwichensis*)	12
Veery (*Catharus fuscescens*)	11
Wood Thrush (*Hylocichla mustelina*)	10
Cape May Warbler (*Setophaga tigrina*)	10
Sora (*Porzana carolina*)	9
American Robin (*Turdus migratorius*)	9
Blackburnian Warbler (*Setophaga fusca*)	8
Clay-colored Sparrow (*Spizella pallida*)	8
Indigo Bunting (*Passerina cyanea*)	8
Great Crested Flycatcher (*Myiarchus crinitus*)	7
Blue-gray Gnatcatcher (*Polioptila caerulea*)	7
Red-winged Blackbird (*Agelaius phoeniceus*)	7
Bobolink (*Dolichonyx oryzivorus*)	7
Thrush (*Catharus* spp.)	6
Brown Thrasher (*Toxostoma rufum*)	6
Tennessee Warbler (*Oreothlypis peregrina*)	6
Scarlet Tanager (*Piranga olivacea*)	6
Song Sparrow (*Melospiza melodia*)	6
Field Sparrow (*Spizella pusilla*)	6
Least Bittern (*Ixobrychus exilis*)	5
Chimney Swift (*Chaetura pelagica*)	5
Red-headed Woodpecker (*Melanerpes erythrocephalus*)	5

APPENDIX. Continued.

Gray-cheeked Thrush (*Catharus minimus*)	5
Golden-winged Warbler (*Vermivora chrysoptera*)	5
Blue-winged Warbler (*Vermivora cyanoptera*)	5
Northern Parula (*Setophaga americana*)	4
Virginia Rail (*Rallus limicola*)	3
Mourning Dove (*Zenaida macroura*)	3
Ruby-throated Hummingbird (*Archilochus colubris*)	3
Eastern Wood-Pewee (*Contopus virens*)	3
Eastern Kingbird (*Tyrannus tyrannus*)	3
Blue Jay (*Cyanocitta cristata*)	3
Winter Wren (*Troglodytes hiemalis*)	3
Bay-breasted Warbler (*Setophaga castanea*)	3
Yellow-breasted Chat (*Icteria virens*)	3
Le Conte's Sparrow (*Ammodramus leconteii*)	3
Grasshopper Sparrow (*Ammodramus savannarum*)	3
Yellow Rail (*Coturnicops noveboracensis*)	2
Eastern Whip-poor-will (*Antrostomus vociferus*)	2
Olive-sided Flycatcher (*Contopus cooperi*)	2
Least Flycatcher (*Empidonax minimus*)	2
Brown Creeper (*Certhia americana*)	2
Golden-crowned Kinglet (*Regulus satrapa*)	2
Northern Mockingbird (*Mimus polyglottos*)	2
Kentucky Warbler (*Geothlypis formosa*)	2
Hooded Warbler (*Setophaga citrina*)	2
Summer Tanager (*Piranga rubra*)	2
Dark-eyed Junco (*Junco hyemalis*)	2
Orchard Oriole (*Icterus spurius*)	2
Common Grackle (*Quiscalus quiscula*)	2
Green Heron (*Butorides virescens*)	1
Black-crowned Night-Heron (*Nycticorax nycticorax*)	1
Lesser Scaup (*Aythya affinis*)	1
King Rail (*Rallus elegans*)	1
Black-bellied Plover (*Pluvialis squatarola*)	1
Spotted Sandpiper (*Actitis macularius*)	1
Least Sandpiper (*Calidris minutilla*)	1
Bonaparte's Gull (*Chroicocephalus philadelphia*)	1
Common Tern (*Sterna hirundo*)	1
Yellow-billed Cuckoo (*Coccyzus americanus*)	1
Red-bellied Woodpecker (*Melanerpes carolinus*)	1
Downy Woodpecker (*Picoides pubescens*)	1
Hairy Woodpecker (*Picoides villosus*)	1
Northern Flicker (*Colaptes auratus*)	1
Philadelphia Vireo (*Vireo philadelphicus*)	1
Horned Lark (*Eremophila alpestris*)	1
Bank Swallow (*Riparia riparia*)	1
European Starling (*Sturnus vulgaris*)	1
Cedar Waxwing (*Bombycilla cedrorum*)	1
Orange-crowned Warbler (*Oreothlypis celata*)	1
Cerulean Warbler (*Setophaga cerulea*)	1
Blackpoll Warbler (*Setophaga striata*)	1
Worm-eating Warbler (*Helmitheros vermivorum*)	1
Eastern Towhee (*Pipilo erythrophthalmus*)	1
Northern Cardinal (*Cardinalis cardinalis*)	1
Purple Finch (*Carpodacus purpureus*)	1
Pine Siskin (*Spinus pinus*)	1

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INFLUENCE OF SEASON AND TIME OF DAY ON MARSH BIRD DETECTIONS

TYLER M. HARMS[1,2] AND STEPHEN J. DINSMORE[1]

ABSTRACT.—Call-broadcast surveys are frequently used to elicit responses of secretive marsh birds and produce greater detection rates than passive surveys. However, little is known about how detection rates of birds from these surveys differ by season and time of day. We conducted call-broadcast surveys for eight focal species at 56 wetlands throughout Iowa from 15 May–13 June 2010 (early season) and from 15 June–10 July 2010 (late season). Our focal species were Pied-billed Grebe (*Podilymbus podiceps*), American Bittern (*Botaurus lentiginosus*), Least Bittern (*Ixobrychus exilis*), King Rail (*Rallus elegans*), Virginia Rail (*Rallus limicola*), Sora (*Porzana carolina*), Common Gallinule (*Gallinula chloropus*), and American Coot (*Fulica americana*). Surveys were conducted in the early morning (30 mins before sunrise to 3 hrs after sunrise) and late evening (3 hrs before sunset to 30 mins after sunset) in accordance with the North American Marsh Bird Monitoring Protocol. We evaluated marsh bird detection rates as a function of a) time of day (morning and evening survey periods), b) season (early and late in the breeding season), and c) wetland size for four species with the greatest detection rates (Pied-billed Grebe, Least Bittern, Virginia Rail, and Sora). We also evaluated the above effects for two species groups; all eight species pooled and all rails pooled. We found significant ($P < 0.05$) effects on the number of detections for Pied-billed Grebe in response to time of day, time of season, and wetland size; Sora, Virginia Rail, all rails, and all species had an effect of time of season only. Understanding seasonal and time-of-day differences in detection rates, as well as area dependence of secretive marsh birds, will refine existing monitoring protocols by allowing researchers to maximize detection probabilities of target species. *Received 10 September 2013. Accepted 2 November 2013.*

Key words: bittern, call-broadcast, coot, detection, gallinule, Iowa, marsh bird, rail.

Secretive marsh birds (e.g., bitterns and rails) are some of the most inconspicuous birds in North America. These birds are difficult to monitor using conventional survey techniques, because they vocalize infrequently and tend to occupy habitats that are densely covered with emergent vegetation (Lor and Malecki 2002). In addition, their crepuscular habits require sampling to occur in the early-morning and late-evening hours. The North American Marsh Bird Monitoring Protocol (Conway 2007, 2011) was established to aid researchers in the development of standardized surveys to effectively monitor these secretive marsh birds. Call-broadcast surveys have been implemented in several studies to elicit responses from marsh birds (Johnson and Dinsmore 1986, Manci and Rusch 1988, Gibbs and Melvin 1993, Lor and Malecki 2002) and produce higher detection rates when compared to passive surveys (Gibbs and Melvin 1993, Erwin et al. 2002, Allen et al. 2004, Conway and Gibbs 2005, DesRochers et al. 2008). However, the effectiveness of call-broadcast surveys can vary temporally (Conway and Gibbs 2001, Rehm and Baldassarre 2007, Nadeau et al. 2008) and by species (Manci and Rusch 1988, Gibbs and Melvin 1993, Lor and Malecki 2002, Soehren et al. 2009). There is a need for additional information on seasonal variation in detection rates and whether detections vary between morning and evening. This information can aid in planning survey efforts to maximize detection probability of the target species.

The North American Marsh Bird Monitoring Protocol (Conway 2007, 2011) instructs researchers to conduct call-broadcast surveys in the morning or evening depending on when birds are most vocal in the study area. A single study found that vocalization probabilities of marsh birds are greater during morning surveys (Nadeau et al. 2008); other studies have shown that such probabilities are greater during evening surveys (Johnson and Dinsmore 1986, Conway et al. 2004). Environmental factors such as temperature, wind speed, and cloud cover may vary with time of day, potentially affecting the vocalization frequency of marsh birds (Nadeau et al. 2008). Vocalization frequencies may vary with time of day at both the individual or species level because of behavioral variation of individual birds, differences in species-specific preferences in timing of calling, and individual breeding status (Conway et al. 1993, Palmeirim and Rabaça 1994). To date, no research has been done to determine the best time of day for surveying marsh birds in the midwestern United States.

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Another goal of call-broadcast surveys for marsh birds is to minimize temporal variation in detection probability (Conway and Gibbs 2001, 2005). In other words, surveys should be conducted during periods of peak detection probabilities with little variation during the survey season. The national monitoring protocol states that optimal timing of surveys should overlap with the breeding seasons of focal marsh bird species in the study area and suggests that surveys be conducted during a 45-day window that varies regionally based on average minimum temperatures in May (Conway 2007, 2011). However, research has found that these survey windows may not be long enough to include peak detection periods for all focal species (Rehm and Baldassarre 2007). In Iowa, for example, American Bitterns (*Botaurus lentiginosus*) and Soras (*Porzana carolina*) arrive and initiate breeding in mid- to late April (Kent and Dinsmore 1996), whereas Least Bitterns (*Ixobrychus exilis*) arrive in mid-May and initiate breeding in late May or early June (Weller 1961). Therefore, the suggested survey window for Iowa (15 Apr–30 May) may not include peak detection periods for all species of marsh birds, especially late breeders like Least Bitterns. An adjustment of survey timing at the regional level may be necessary to account for seasonal differences in detection of target species.

Our objective was to examine the effects of: (1) time of day, (2) time of season, and (3) wetland size on the detection rates of secretive marsh birds in Iowa. This information will help refine survey timing for secretive marsh birds in the midwestern United States.

METHODS

Study Area.—We surveyed marsh birds at wetlands in the Des Moines Lobe of north-central and northwestern Iowa (Prior 1991; Fig. 1). We used the National Wetlands Inventory (NWI; U.S. Fish and Wildlife Service 2009) to select our sites. We considered both natural and constructed wetlands from the Aquatic Bed (AB), Emergent (EM), and Unconsolidated Bottom (UB) classes of the Palustrine system (Wilen and Bates 1995). Wetlands within these classes fit one or more of the following general habitat criteria required by our target species: (1) shallow water (<1 m deep), (2) closed basins (no inflow or outflow), (3) surrounded by few or no trees, and/or (4) the presence of emergent vegetation. Most wetlands were permanent or semi-permanent, although

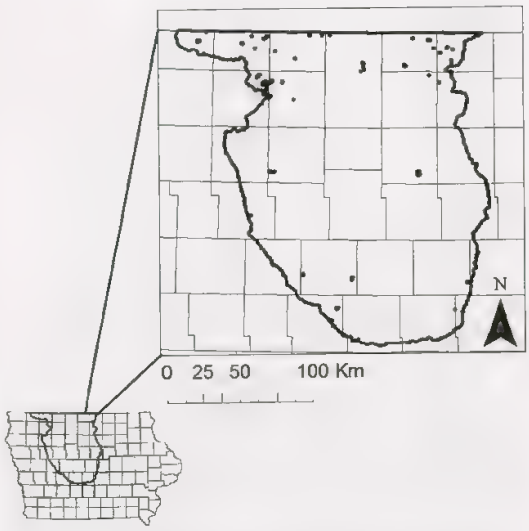

FIG. 1. Location of surveyed wetlands (points) within the Des Moines Lobe (bold line) region of Iowa, 2010.

some temporary or seasonal wetlands were also selected (Stewart and Kantrud 1971). Most wetlands contained a mix of emergent vegetation that included cattail (*Typha* spp.), sedge (*Carex* spp.), river bulrush (*Scirpus fluviatilis*), soft-stem bulrush (*Schoenoplectus tabernaemontani*), or reed canary grass (*Phalaris arundinacea*). Water depths ranged from 0–115 cm at survey points within wetlands.

Site Selection and Surveys.—Using Hawth's Analysis Tools for ArcGIS (Beyer 2004), we randomly selected wetlands from the NWI database. To facilitate access for surveys, we selected only wetlands that were on public lands. We stratified wetlands into six size classes based on area (≤5 ha, >5–10 ha, >10–20 ha, >20–30 ha, >30–40 ha, and >40 ha) to facilitate an equal representation of wetlands of different sizes and ensure that potential area-dependent species were sampled. We randomly selected 10 wetlands from each size class (Brown and Dinsmore 1986), with the exception of the 30–40 ha size class where only six wetlands were selected because of the small number (n = 11) of wetlands within that size class. We randomly assigned a fixed number of survey points 400 m apart to wetlands within each size class to allow for maximum coverage of each wetland and to minimize double-counting birds (Conway 2007, 2011). We assigned one point to both the <5 ha and >5–10 ha size classes, two points to the >10–20 ha size class, three points to the >20–30 ha size class, four

points to the >30–40 ha size class, and five points to the >40 ha size class.

We conducted unlimited-radius point counts with call-broadcast surveys from 15 May–10 July 2010. We conducted surveys for eight focal species of marsh birds in accordance with the North American Marsh Bird Monitoring Protocol (Conway 2007, 2011). The eight focal species included Pied-billed Grebe (*Podilymbus podiceps*), American Bittern, Least Bittern, King Rail (*Rallus elegans*), Virginia Rail (*Rallus limicola*), Sora, Common Gallinule (*Gallinula chloropus*), and American Coot (*Fulica americana*). Using an MP3 player (SanDisk Sansa Clip 1 GB, SanDisk Corporation, Milpitas, CA, USA) attached to a pair of amplified speakers (Panasonic Model RPSPT70, Panasonic Corporation, Secaucus, NJ, USA), we broadcast the call sequence at 90 dB 1 m from the source (Conway 2007, 2011). We placed the speakers 0.5 m from the substrate (ground or water surface) and pointed them towards the interior of the wetland. The call-broadcast sequence was obtained from the North American Marsh Bird Monitoring Program coordinator (Conway 2007, 2011) and consisted of a 5-min passive listening period followed by 8 min of vocalizations. Each minute of the 8-min call-broadcast period corresponded to one species and consisted of 30 secs of vocalizations followed by 30 secs of silence. Vocalizations were ordered by species dominance (Least Bittern, Sora, Virginia Rail, King Rail, American Bittern, Common Gallinule, American Coot, Pied-billed Grebe) to minimize scaring birds prior to their respective sequence (Conway 2007, 2011). We recorded all visual and aural detections of all focal species at each survey point. Using a laser rangefinder, we measured the linear distance to each individual bird when it was first detected. We refrained from conducting surveys during periods of rain or when wind speeds exceeded 12 km/hr. Most survey points were accessed by foot, although we used a canoe to reach points on some larger wetlands.

To assess time-of-day differences in detection rates, we conducted paired surveys at each wetland during both morning (30 mins before sunrise to 3 hrs after sunrise) and evening (3 hrs before sunset to 30 mins after sunset) survey periods. We conducted surveys during consecutive survey periods (morning-evening or evening-morning) to minimize any daily variation in detections of birds (Nadeau et al. 2008), and the order in which we conducted morning and evening surveys was varied so that one survey was not always conducted prior to the other (Conway et al. 2004). We split the survey season into early season (15 May–14 Jun) and late season (15 Jun–14 Jul) and conducted paired surveys at each wetland during both seasons. The early survey season encompassed both survey windows (15 Apr–31 May and 1 May–15 Jun) established for Iowa in the North American Marsh Bird Monitoring Protocol (Conway 2007, 2011) and the late season included the 1-month period after established survey windows during which we hypothesized birds were still vocal. This allowed us to compare the number of marsh bird detections between surveys conducted during the established survey windows and after the established survey windows. To standardize the time between surveys, we conducted late-season surveys about a month (within 3 days) after early-season surveys. We randomized the order in which points were surveyed at each visit to minimize variation in vocalization frequency of individual birds at survey points and minimize dependence among survey points.

Statistical Analyses.—Using generalized linear mixed-effects models (PROC GLIMMIX; SAS Institute 2002) we examined the effects of time of day (TIME OF DAY), time of season (TIME OF SEASON), and wetland size (WETSIZE) on the number of detections at each survey point. We included wetland size in our analyses because some marsh bird species are area-dependent and because wetland size could influence the number of detections at the wetland because of density-dependence effects (Brown and Dinsmore 1986, 1988; Grover and Baldassarre 1995; Rehm and Baldassarre 2007; Harms and Dinsmore 2013). Because our data were over-dispersed counts, we fit models using a Poisson-log normal probability distribution and a log (ln) link function (P. M. Dixon, pers. comm.). Also known as mixed Poisson regression models, these models assume that the conditional distribution of the response is Poisson distributed with a random mean, which is dependent on the normally-distributed random effects (Weems and Smith 2004). We included a random effect on each individual visit to each wetland (WETLAND*TIME OF DAY*TIME OF SEASON) and random effects on wetland (WETLAND), survey point (POINT), the interaction of wetland and time of day (WETLAND*TIME OF DAY), and the interaction of wetland and time of season (WETLAND*TIME OF SEASON) to

TABLE 1. Number of detections of marsh bird species and species groups by survey period during call-broadcast surveys in Iowa, 2010.

Species	Early season		Late season		Total
	Morning	Evening	Morning	Evening	
Pied-billed Grebe	48	54	49	10	161
Least Bittern	22	17	13	28	80
Virginia Rail	54	55	40	36	185
Sora	35	23	5	1	64
Rails	95	80	51	38	264
All species	180	199	126	91	596

further account for variation in the model. Models rarely considered more than two of the random effects as having a significant contribution to variance in the data. We considered effects significant at $P \leq 0.05$. For those models that yielded a significant interaction between time of season and time of day, we conducted additional analyses to explore the interaction by splitting the dataset into early and late season detections and then evaluating the time-of-day effect on detections from each season.

As we were interested in determining the degree to which birds vocalize diurnally and seasonally, we used the total number of detections as our response variable. This means that we included all vocalizations in the analyses whether it was one bird vocalizing three times or three individual birds vocalizing once. Although this approach does not account for the number of birds at each survey point, we were careful not to double count birds at each survey point. This was a relatively easy task because only rarely were there >3 detections of a species at one point. We attempted to estimate mean patch abundance and detection probabilities using the model framework outlined by Royle and Nichols (2003). However, our data did not work well with this model and we rarely obtained numerical convergence. We assumed that detection probability was increased in our study by the use of call-broadcast surveys (Gibbs and Melvin 1993, Conway and Gibbs 2005). We also assumed constant detection probability across survey sites, because sites contained similar habitat and because habitats were open with little vegetation to act as a barrier to bird detections. Time of day and time of season were categorical variables (1 or 2) corresponding to morning and evening survey periods and early and late in the survey season, respectively.

We modeled the number of detections versus fixed effects for four of our focal species. We chose these species to compare results between three breeding species (Pied-billed Grebe, Least Bittern, and Virginia Rail) and a migrant (Sora). Each fixed effect was modeled on the number of detections individually; we did not consider a full model that included all fixed effects on the number of detections. Because of the low number of detections (<10), we could not model the number of detections for American Bittern, King Rail, or Common Gallinule. We chose not to include American Coot, because many individuals were visually detected and their response to call-broadcasts was problematic. We also modeled the number of detections for all rails combined (King Rail, Virginia Rail, Sora, and Common Gallinule) and for all eight species pooled.

RESULTS

We surveyed a total of 56 wetlands (136 points) from both 15 May–14 June (early season) and 15 June–10 July (late season) 2010 (Fig. 1). The number of detections was greater during the early season (n = 379) than during the late season (n = 217), and we had more detections during morning survey periods (n = 306) than during evening survey periods (n = 290; Table 1).

We found that for three species (Pied-billed Grebe, Virginia Rail, and Sora) and both species groups, birds were more vocal early in the survey season than late in the survey season (Table 2). For Pied-billed Grebes and all species pooled, we found wetland size to have a significant positive effect on species detection rates, with detection rates of birds greater at larger wetlands than at smaller wetlands. However, the overall effect of wetland size on detection rates was small. We also found a significant effect of the interaction of time

TABLE 2. Individual model estimates (95% CI) for each fixed effect by marsh bird species and species groups from call-broadcast surveys in Iowa, 2010. Significant effects ($P < 0.05$) denoted with *. For time of season, we report the effect of early season compared to late season. For time of day, we report the effect of morning survey period compared to evening survey period.

Species	Time of season	Time of day	Wetland size
Pied-billed Grebe	0.55 (0.23, 0.87)*	0.20 (−0.07, 0.47)	0.01 (0.001, 0.013)*
Least Bittern	−0.14 (−0.56, 0.26)	−0.30 (−0.69, 0.10)	0.005 (−0.002, 0.01)
Virginia Rail	0.38 (0.12, 0.65)*	−0.19 (−0.45, 0.07)	0.003 (−0.002, 0.01)
Sora	1.87 (1.17, 2.56)*	0.26 (−0.19, 0.72)	0.01 (−0.006, 0.01)
Rails	0.63 (0.37, 0.88)*	−0.04 (−0.26, 0.18)	0.01 (−0.002, 0.01)
All species	0.59 (0.42, 0.76)*	−0.02 (−0.16, 0.12)	0.01 (0.002, 0.012)*

of season and time of day on all individual species except Least Bittern, and for both species groups. Further analysis of the interaction term for these species and species groups only yielded a significant effect of time of day late in the survey season for Pied-billed Grebes ($P = 0.014$). Pied-billed Grebes were more vocal during the morning survey period than the evening survey period ($\beta_{Morning} = 0.23$, 95% CI 0.05, 0.42; Table 3). We found no significant effects of time of day by season for any other species or species group, although these effects were poorly estimated (Table 3).

DISCUSSION

Our work has shown that marsh bird response rates vary seasonally, by time of day, and in response to wetland size, although these patterns were not consistent across species. This has important implications for designing future marsh bird surveys, especially with regard to survey windows for each species. Seasonal differences in detection rates have been observed for several species of marsh birds (Spear et al. 1999, Rehm and Baldassarre 2007). These differences, however, can vary geographically (Rehm and Baldassarre 2007). In this study, birds vocalized more frequently early in the survey season than late in the survey season. The explanation for this finding varies by species. Pied-billed Grebes and Virginia Rails are regular breeders in Iowa and their peak breeding seasons overlap with the early portion of the survey period. Virginia Rails frequently vocalize during the breeding season (Glahn 1974, Conway 1995), but are mostly silent during migration (Griese et al. 1980, Kaufmann 1989). Similarly, Pied-billed Grebes frequently vocalize during the breeding season when establishing territories and during courtship (Glover 1953, Muller and Storer 1999), but vocalize less frequently outside of the breeding season depending on geographic location (Palmer 1962, Muller and Storer 1999). We expected the distribution of detections of both Pied-billed Grebes and Virginia Rails to be non-linear. That is, birds vocalize frequently during the breeding season, infrequently when on the nest or with young and more often again later in the survey season at the potential start of a second nesting attempt. Gibbs and Melvin (1993) found that the probability of response for both Pied-billed Grebes and Virginia Rails peaked from 16–31 May, decreased from 1–30 June, and then increased again from 1–15 July. If a similar pattern occurs in Iowa, it could diminish our ability to find differences in the detection rate between early and late in the survey season. Detections for both Pied-billed Grebes and Virginia Rails peaked early in the survey season and decreased over time with no evidence of an increase late in the survey season. Soras commonly vocalize during migration (Kaufmann 1983, 1989; Johnson and Dinsmore 1986) and are common migrants throughout Iowa but only

TABLE 3. Model estimates (95% CI) of the effect of morning survey period compared to evening survey period for both early and late season. Only those species and species groups with a significant ($P < 0.05$) effect in the individual model of the interaction of time of season and time of day are displayed. Significant ($P < 0.05$) effects from the model that included only season and time of day are denoted with *.

Species	Early season	Late season
Pied-billed Grebe	−0.17 (−0.51, 0.18)	0.87 (0.38, 1.36)*
Virginia Rail	−0.28 (−0.62, 0.06)	−0.06 (−0.47, 0.34)
Sora	0.21 (−0.28, 0.71)	0.56 (−0.67, 1.79)
Rails	−0.09 (−0.36, 0.19)	0.06 (−0.32, 0.43)
All species	−0.10 (−0.28, 0.08)	0.13 (−0.11, 0.37)

infrequently breed in the northern half of the state (Melvin and Gibbs 1996). This explains why the detection rate of Soras met our *a priori* expectations of strong seasonal variation in detection rates, with a peak early in the survey season and a steady decline thereafter.

Our data indicate that time of day alone did not affect the detection rate of most species of marsh birds. We were surprised by this result, because other studies have found that vocalization frequencies of marsh birds vary by time of day (Johnson and Dinsmore 1986, Conway et al. 2004, Nadeau et al. 2008). Variation in vocalization frequency of marsh birds is often attributed to temperature (Spear et al. 1999, Nadeau et al. 2008), because higher temperatures during the evening survey period may decrease activity levels of birds (Robbins 1981). We found a time-of-day effect on the number of detections for Pied-billed Grebes only, but this effect was significant only late in the survey season. As expected, the number of detections of Pied-billed Grebes was greater during the morning survey period than the evening survey period but only during late season. Gibbs and Melvin (1993) also observed that detection probabilities of Pied-billed Grebes were relatively high during morning surveys, although no previous studies have compared detection probabilities of Pied-billed Grebes between morning and evening survey periods. We attribute increased detections of Pied-billed Grebes during the morning survey period late in the season to weather conditions. Late in the survey season, temperatures ranged from 12.3–25.4 °C during morning survey periods and 19.4–33.0 °C during evening survey periods with a mean difference of 6.6 °C. This suggests that Pied-billed Grebes are most active and vocal during cooler times of the day (e.g., morning hours) late in the season because of generally warmer temperatures during this time of year. It is difficult to ascertain why higher evening temperatures affect the detection rate of Pied-billed Grebes and not that of other species. Pied-billed Grebes spend a majority of their time on open water, whereas bitterns and rails spend their time in dense, tall stands of emergent vegetation (TMH, pers. obs.).

Perhaps Pied-billed Grebes are most active during cooler, morning hours because they are more exposed to direct sunlight. Rails and bitterns are protected from the sun by tall vegetation, and therefore can remain active during the warmer hours of the day. In addition to our findings for Pied-billed Grebes, we found a significant effect of the interaction of time of season and time of day for Virginia Rails, Soras, all rails, and all species pooled, although when modeled separately, the effect of time of day by season for these species and species groups was not significant. Our results illustrate that time of season alone affected detection rates for all species except Least Bittern and both species groups. Therefore, time of season is driving the significance of the interaction and not time of day. Examination of these effects showed that detection rates were higher in the morning during both seasons for Soras, were higher in the evening during early season and in the morning during late season for all rails and all species, and higher in evening during both seasons for Virginia Rails. We conclude that the non-significance of these effects is a result of poor estimation of the time-of-day effects. However, they still demonstrate that most birds are more vocal in the morning late in the season, probably to avoid warmer temperatures (Spear et al. 1999, Nadeau et al. 2008). In contrast, Virginia Rails are more vocal in the evening both early and late in the season. Virginia Rails are often most vocal during a 3-hr period surrounding both dawn and dusk, and will also vocalize throughout the night during the peak of the breeding season (Conway 1995). This result coincides with that of Johnson and Dinsmore (1986) who found that night counts produced greater response rates for Virginia Rails during the breeding season.

We did not find effects of time of season or time of day on the detection rate for Least Bitterns. Least Bitterns vocalize infrequently (Bogner and Baldassarre 2002b), and it is debatable whether call-broadcast surveys are effective at increasing detection probabilities of these birds. Some studies have shown that call-broadcasts are effective at eliciting responses of Least Bitterns (Swift et al. 1988, Gibbs and Melvin 1993, Bogner and Baldassarre 2002b), whereas other studies have shown call-broadcasts to be ineffective (Manci and Rusch 1988, Tozer et al. 2007). Although we did not address the effectiveness of call-broadcasts at increasing detections of Least Bitterns in this study, the number of detections (n = 80) was relatively low compared to other species. In addition, Bogner and Baldassarre (2002b) suggested that call-broadcast sequences consist of >1 min of calls

by Least Bitterns to effectively stimulate the bitterns to respond. Our call sequence contained 30 secs of calls by Least Bitterns. The unknown effectiveness of call-broadcast surveys and our small sample size could explain why we did not find any seasonal or time-of-day effects on the number of detections of Least Bitterns.

Wetland size significantly affected our detection rates of Pied-billed Grebes and all species pooled, indicating that detection rates were greater at larger wetlands than at small wetlands. We suspect this may be a result of density-dependent effects for at least some species, with larger wetlands perhaps having more individuals and territorial interactions that led to increased vocalization rates and greater detection probability. Studies have found that some species of marsh birds, including Pied-billed Grebes (Brown and Dinsmore 1986, Osnas 2003) and Least Bitterns (Brown and Dinsmore 1986, Moore et al. 2009, Harms and Dinsmore 2013), are area-dependent, while other species such as Virginia Rails and Soras are area-independent (Brown and Dinsmore 1986). Larger wetlands provide desired habitat characteristics for some species (e.g., deeper water for Pied-billed Grebes), support greater densities of breeding pairs (Bogner and Baldassarre 2002a), and foster increased species diversity (Brown and Dinsmore 1986, Fairbairn and Dinsmore 2001, Craig 2008). Because we surveyed an equal number of wetlands within each size class and surveyed all wetlands during both times of day and both seasons, we do not expect wetland size to compound effects of time of day or time of season. Larger wetlands likely harbor more birds, thus increasing the detection rates of different species.

The North American Marsh Bird Monitoring Protocol (Conway 2007, 2011) suggests a survey window of 15 April–30 May for Iowa based on average minimum temperatures in May. We extended our survey season to 10 July to determine if there was a justification for extending the survey window for Iowa. As a result, we detected nearly half of the total number of birds (n = 296) after 30 May, illustrating that the survey window for Iowa can be extended to increase detections of target species. Rehm and Baldassarre (2007) found similar results in their study based in New York and also suggested that the survey window be extended to incorporate peak detection periods for all species.

Interspecific seasonal variation of peak detection periods should be considered when conducting call-broadcast surveys, especially when surveying for both breeding species and migrants. If time is a limiting factor, surveys should be conducted early in the survey season, because this is when marsh birds are most vocal and detections of target species can be increased. However, caution should be used as undersampling of some species may still occur. Surveys for Pied-billed Grebes should also be limited to the morning survey period. In Iowa, we suggest extending the survey window past that recommended by the North American Marsh Bird Monitoring Protocol to increase the number of detections of marsh birds. Minimally, this period should be extended to 15 June, although the exact date will depend on the species being surveyed, average temperatures that affect arrival times and breeding phenology of birds, and the time available for conducting surveys.

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RETENTION RATES OF GLUE-ATTACHED RADIO-TRANSMITTERS ON TWO SMALL BIRD SPECIES WITH CONTRASTING LIFE HISTORIES

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ABSTRACT.—Recent advances in radio-transmitter technology have produced sub-gram transmitters which allow small birds to be radio-tracked so that researchers can ascertain information on species movement and behavior to inform conservation and management plans. However, the ability to study some species remains limited by practical problems with transmitter attachment. As a result, improvements in design may be hindered by underreporting of retention rates and attachment issues. We monitored retention rates for glue-attached radio-transmitters on two bird species in southern Ontario with different life histories. Mean retention time for Chimney Swifts (*Chaetura pelagica*) was ≥25.1 days (± 12.8 SD, n = 12, May–Aug 2010 and 2011), while for Bobolinks (*Dolichonyx oryzivorus*) we estimated mean retention time at under 24 hrs (n = 15, May–Jul 2011). We discuss potential reasons for this disparity and suggest improvements to transmitters and attachment methods for short-term use on small birds where tag retention and damage may be problematic, as Bobolinks were capable of removing transmitters and breaking antennas which, in some cases, rendered the devices inoperative. We collated retention estimates from published studies that marked birds with glue-attached radio-transmitters; these studies used a wide range of methods with varying success on different species, however, few studies specifically examined the effects of alterations in glue attachment methods on retention. We encourage researchers to report retention rates to improve the use of resources in other studies and enable advancements that will augment the potential of existing radiotelemetry technology. *Received 17 June 2013. Accepted 24 September 2013.*

Key words: *Chaetura pelagica*, *Dolichonyx oryzivorus*, glue-attached, radiotelemetry, retention, sub-gram radio-transmitters, transmitter removal.

Marking animals to facilitate later recognition of individuals has been central to data collection for countless wildlife studies. Marking methods have been especially diverse in avian research, where techniques such as applying unique identifying bands to legs, necks, or wings (Lincoln 1921, Hewitt and Austin-Smith 1966, Menu et al. 2000), combinations of colored leg-bands (Wood 1945), coloring agents to feathers (Donehower and Bird 2005, Tupper et al. 2009), and feather attachments (Best 1990) are routinely used. Such methods often require substantial effort to collect field data on a fairly coarse temporal and spatial scale. However, recent technological advances have enabled much finer resolution to location data, including increasingly smaller GPS devices, geolocators, and radio-transmitters.

Radiotelemetry is used widely across many taxa to investigate demographic, physiological, and behavioral parameters and can often provide information essential for conservation and management objectives (Kenward 2001, Millspaugh and Marzluff 2001). Recent miniaturization of radio-transmitters has allowed even small birds to be marked with sub-gram tags using established attachment methods (Rappole and Tipton 1991, Woolnough et al. 2004, Mong and Sandercock 2007). However, despite remarkable advances in transmitter technology, practical problems are still commonplace though underreported (Hill and Elphick 2011), particularly issues with tag retention (Woolnough et al. 2004, Fisher et al. 2010). This is a non-trivial issue that requires greater empirical attention, as the expenses associated with purchasing telemetry equipment and radio-transmitters are substantial for most projects, and employing faulty methods that require further efforts puts additional stress on birds. Information is needed to better identify species or their attributes that make telemetry efforts problematic (Barron et al. 2010, Hill and Elphick 2011). It is also important to examine how retention differs for specific transmitter attachment methods and modifications, which will assist future studies that rely on telemetry. Glue-attached tags are desirable for short-term study, but there are many variations to attachment methods in the literature with little empirical support for determining which are the superior techniques.

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Here, we assess retention rates of glue-attached radio-transmitters (avian Nanotags®, Lotek Wireless Inc., Newmarket, ON) when applied to two species that exhibit contrasting life histories: Chimney Swifts (*Chaetura pelagica*) and Bobolinks (*Dolichonyx oryzivorus*). Chimney Swifts are non-passerine aerial insectivores that spend most of the day in flight, landing only to nest or roost, and are rarely in contact with any substrate (Cink and Collins 2002); like most aerial insectivores, they have a small beak with little biting force. In contrast, Bobolinks spend a large amount of time in contact with grassland vegetation, and possess a strong seed-crushing beak that enables them to remove some leg-bands (Balph 1979). Both species are classified as threatened in our study area (federally in Canada and provincially in Ontario), and the ability to track movement for these species has significant bearing on conservation and management decisions. Information on habitat use by Chimney Swifts is needed given the expansion of urban habitat used by swifts which may require them to travel farther from nests and roosts to acquire resources, potentially reducing their fitness (e.g., Britschgi et al. 2006). Similarly, information is needed concerning dispersal patterns and prospecting behavior of Bobolinks (e.g., Shustack et al. 2010), which are only feasible to study using radio-telemetry.

We attached radio-transmitters with glue to clipped feathers in the interscapular area of Chimney Swifts and Bobolinks. In both species, we expected retention times suitable for short-term study (about 2–3 weeks), because of various successful studies on other small birds; however, we report a large discrepancy in retention rates for these two species. We describe possible influencing factors and discuss recommendations to improve the use and design of these tags for species with lower tolerance for attachments. Further, we examine retention estimates in the literature for studies that attempted to radio-track various bird species using glue-attachment methods.

METHODS

Radiotelemetry.—From May–July of 2011, we used mist-nets to capture breeding Bobolinks in/near male territories in hayfields of Peterborough and Kawartha Lakes counties of Ontario, Canada (centered on 44° 20′ N, 78° 30′ W). We used a modified hoop-net (Colvin and Hegdal 1986, Wheeler 2012) to capture Chimney Swifts as they left chimneys used for nesting in Guelph, Ontario, Canada (centered on 43° 32′ N, 80° 17′ W) from May–August of 2010 and 2011. We captured and handled all Bobolinks according to procedures approved by the Ontario Ministry of Natural Resources' Animal Care Committee (protocol #11-256), and Chimney Swifts according to procedures approved by the Trent University Animal Care Committee (protocol #10-053).

We outfitted adult Bobolinks and Chimney Swifts with avian Nanotags® (model NTQB-3-2, Lotek Wireless Inc.; Fig. 1) that had a manufacturer-reported mean battery life of 43 days. Each tag weighed 0.64 g, which represents 1.9% of the mean breeding weight of male and 2.2% of female Bobolinks (Meanley 1967), and 2.9% of the average weight of an adult Chimney Swift (Sibley 2000). After clipping several feathers in the interscapular region, we activated transmitters, verified activation, and glued them with an ethyl cyanoacrylate adhesive to the clipped feather shafts (*sensu* Raim 1978, Johnson et al. 1991; Fig. 1). For Chimney Swifts, transmitters were first glued to a small piece of cotton fabric trimmed to slightly larger than the transmitter silhouette. A fabric interface was not used for Bobolinks and the transmitter was glued directly to the feather shafts. This was not expected to affect retention, because numerous studies have omitted fabric when gluing to clipped feathers with similar retention rates to those that used it (Table 1), and our comparative study here was not designed with an objective of directly comparing retention times. Transmitters were attached by one investigator in each respective study. Devices were held in place for ~3 mins and adherence was deemed adequate when the tag could not be removed by gentle pulling. We strove for transmitter retention to be nearly as long as the battery-life; retention any longer than this was unnecessary as transmitter loss was expected with molting prior to migration. Harness attachment methods have longer retention rates, but were considered excessive for our short-term studies, and may reduce annual survival (Mong and Sandercock 2007). Following application of the tags, we fitted birds with uniquely-numbered United States Geological Survey aluminum leg bands (issued by the Canadian Wildlife Service) and released them at the site of capture.

At least once every 48 hrs, we attempted to track all radio-tagged Bobolinks from vehicles and on foot with a 3-element Yagi antenna

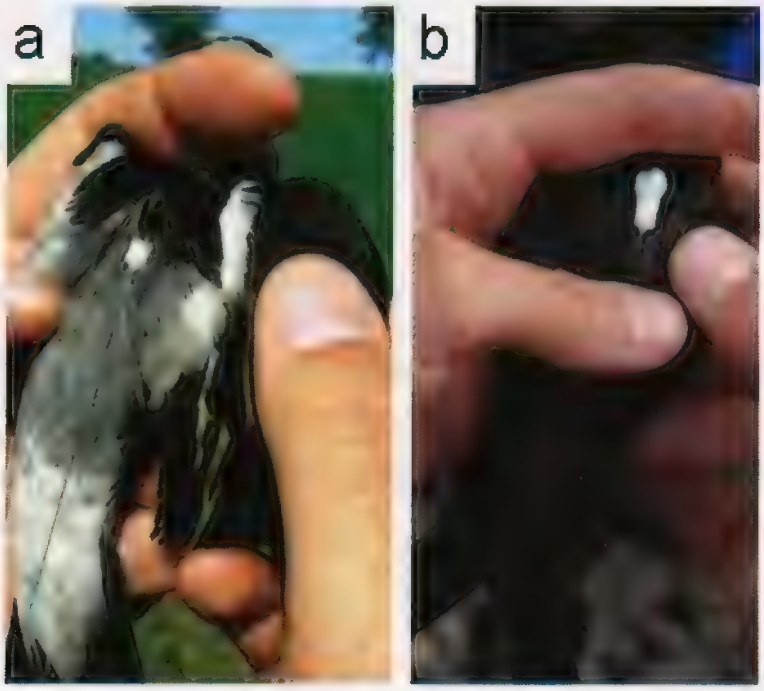

FIG. 1. Miniature radio-transmitters attached with cyanoacrylate glue to clipped feathers on the interscapular region of (a) male Bobolink (*Dolichonyx oryzivorus*) and (b) Chimney Swift (*Chaetura pelagica*).

attached to either an R-1000 handheld receiver (Communication Specialists Inc., Orange, CA, USA) or an SRX-600 data-logging receiver (Lotek Wireless Inc.). The estimated range for signal detection was up to ~400 m for Bobolinks. We tracked Chimney Swifts continuously using a stationary antenna array comprised of four 9-element Yagi antennas, one pointing in each cardinal direction, attached to an SRX-600 data-logging receiver through an ASP-8 multiple antenna switching unit. We programmed the receiver to switch antennas in a pre-determined order, completing a full detection cycle of all directions every 21.6 secs. This array was erected on the roof of City Hall in downtown Guelph and, because of its substantial elevation, could detect signals up to ~3.5 km in all directions (Wheeler 2013). Chimney Swifts were tracked until signals were no longer detected following transmitter loss, battery failure, or migration from the area.

Literature Search.—To compile estimates of retention for transmitters attached to birds with glue-on methods (*sensu* Raim 1978), we used the online search-engine ISI Web of Science, current to January 2013, with the terms '(radio* OR *transmitter* OR *telemetry* OR *tag*) AND (*glue* OR adhesive* OR cement) AND (bird* OR avian)' in a topic search. We included other references that were found incidentally and excluded studies that tagged altricial young because parents are generally the main cause of tag loss through removal (Mattsson et al. 2006, Fisher et al. 2010).

RESULTS

We captured and radio-tagged 15 Bobolinks (10 males, 5 females) and 13 Chimney Swifts (sex not discernible). Chimney Swifts had satisfactory retention rates; only one tag was lost, which occurred immediately after application, likely a result of imperfect gluing, and it was recovered in a grassy area near the capture/release site. The remaining 12 tags on Chimney Swifts had a mean retention time of ≥25.1 days (± 12.8 SD, minimum transmission time 2.4 days, maximum 29.6 days), which compares to adequate rates noted for glue-attached tags on several passerine and non-passerine species (Table 1). This represents a conservative estimate of retention, as transmitters remained attached until Chimney Swifts migrated from the area or batteries failed.

Retention rates on male and female Bobolinks were completely insufficient; mean retention time

TABLE 1. A comparison of published studies that reported retention times of glue-attached radio transmitters. Studies primarily used the attachment method described by Raim (1978) where transmitters were glued to clipped feathers in the interscapular region of adult birds with latex-based eyelash glue and a fabric interface glued between the transmitter and feather shafts; where studies deviated from this method, their modification is presented. Retention times are generally listed as mean number of days ± either SE or SD followed by a range of values, and sample size is provided where available, otherwise retention times are listed as presented in the original paper. Retention time is indicated as ≥ when investigators ceased tracking birds before transmitters were lost or failed. Sample size is provided when available. Studies that tagged altricial young were not considered here, because parents are generally the main cause of tag loss through removal.

Species	Retention time	Sample size	Attachment modification
Alectura lathami[a]	~21–28 days	-	Glued to skin; no fabric; superprecocial young
Bartramia longicauda[b]	40 days (95% CI = 17–96 days)	12	Glued (to clipped feathers) on the lower back with cyanoacrylate; no fabric
Bartramia longicauda[b]	26 days (95% CI = 17–42 days)	25	Glued to uncut feathers on lower back with cyanoacrylate; no fabric
Bartramia longicauda[b]	7 days (95% CI = 4–11 days)	16	Glued to skin on lower back with cyanoacrylate; no fabric
Brachyramphus brevirostris[c]	10.5 ± 5.2 days (SD)	20	Glued to uncut feathers with cyanoacrylate; no fabric
Calidris alpina[d]	>49 days	29	Glued (to clipped feathers) on the lower back with epoxy; no fabric
Calidris mauri[d]	>49 days	60	Glued (to clipped feathers) on the lower back with epoxy; no fabric
Cardinalis cardinalis[e]	5 ± 0.2 days (SE)	16	Cyanoacrylate glue
Chaetura vauxi[f]	~14–28 days	30	Glued to skin with Skin-Bond cement; no fabric
Charadrius alexandrinus nivosus[g]	≥1–2 months	18	Glued to skin on lower back with cyanoacrylate; no fabric
Chiroxiphia caudata[h]	25% lost <20 days, 55% retained >21 days	69	Glued to skin
Chiroxiphia caudata[h]	50% lost <6 days	6	Latex-free eyelash glue
Cyanocitta cristata[e]	≥20 ± 0.5 days (SE)	24	Cyanoacrylate glue
Fratercula arctica[i]	≥31.0 ± 7.30 days (SE)	4	Glued to trimmed feathers with epoxy; no fabric
Geothlypis trichas[j]	Median 24 days	7	Glued to skin
Geothlypis trichas[j]	Range 0–3 days	-	Glued to skin; no fabric
Hirundo rustica[k]	1–4 days	4	Glued to skin with Skin-Bond cement; no fabric
Limnodromus scolopaceus[l]	20.3 ± 8.5 days (SD)	32	Glued (to clipped feathers) on the lower back with epoxy; no fabric
Meleagris gallopavo[m]	27.6 ± 0.8 days (SE)	20	Glued to skin with cyanoacrylate; precocial young
Meleagris gallopavo intermedia[n]	20.4 ± 8.3 days (SD)	34	Glued to skin with cyanoacrylate; no fabric; precocial young
Molothrus ater[o]	~10–14 days (range 0–24 days)	~40	
Molothrus ater[p]	≥0–21 days	≥23	Epoxy glue
Phasianus colchicus[q]	>10 days	13	No fabric; precocial young
Phylidonyris novaehollandiae or *Phylidonyris nigra*[r]	38% retained >4 days (range 0–23 days)	21	
Pyriglena leucoptera[h]	15.5 days	25	Glued to skin
Pyriglena leucoptera[h]	75% lost <5 days	8	Latex-free eyelash glue
Sclerurus scansor[h]	32 days	23	Glued to skin
Setophaga kirtlandii[j]	6.2 ± 2.52 days (SD)	5	Glued to skin
Setophaga kirtlandii[j]	9.86 ± 7.27 days (SD)	7	Glued to skin with Skin-Bond cement
Sternula antillarum athalassos[g]	≥1–2 months	20	Glued to skin on lower back with cyanoacrylate; no fabric
Sternula antillarum browni[s]	8–12 days	4	Glued to skin with cyanoacrylate; no fabric
Sturnus vulgaris[t]	25% retained 24 days	8	Glued to skin with cyanoacrylate

TABLE 1. Continued.

Species	Retention time	Sample size	Attachment modification
Toxostoma rufum[e]	≥16 ± 0.6 days (SE)	15	Cyanoacrylate glue
Turdus migratorius[c]	≥19 ± 0.2 days (SE)	59	Cyanoacrylate glue
Uria aalge[u]	~10–20 days	14	Resin glue; no fabric
Zenaida asiatica[v]	53% 9.3 ± 7.4 days (SD) 47% ≥ 30 days	30	Epoxy glue; vinyl patch instead of fabric
Zenaida macroura[w]	39% retained >63 days	39	Cyanoacrylate glue; vinyl patch instead of fabric

[a] Göth and Jones 2001.
[b] Mong and Sandercock 2007.
[c] Romano et al. 2007.
[d] Warnock and Warnock 1993.
[e] Johnson et al. 1991.
[f] Bull and Blumton 1997.
[g] Hill and Talent 1990
[h] Hansbauer and Pimentel 2008.
[i] Anker-Nilssen and Aarvak 2009.
[j] Sykes et al. 1990.
[k] Brigham 1989.
[l] Takekawa et al. 2002.
[m] Bowman et al. 2002.
[n] Spears et al. 2002.
[o] Raim 1978.
[p] Dufty Jr. 1982.
[q] Kenward et al. 1993.
[r] O'Connor et al. 1987.
[s] Massey et al. 1988.
[t] Woolnough et al. 2004.
[u] Wanless et al. 1985.
[v] Small et al. 2004.
[w] Schulz et al. 2001.

was likely <1 day, as most tags appeared to be removed or disabled immediately after attachment (within 1 hr) and thus, tag loss and damage-induced transmitter failure was estimated at 100% as no Bobolinks were successfully radio-tracked. Three signals, all on male Bobolinks, were never redetected after attachment, although initial activation was confirmed for all tags. In two cases, both within 30 mins of release, we observed (with 20–60 × spotting scopes) Bobolinks with radio-transmitters that had the antenna broken off very close to the transmitter body, which rendered them inoperative with no signal detected at close range. Thus, at least two of the three tags where the signal was not redetected were because of damage and not bird dispersal from the site. However, the majority of tags were assumed to be removed intact, as the remaining 12 signals were tracked repeatedly to the same location first acquired within ~1–24 hrs of attachment though no bird was found (we noted several signals were weakened, suggesting damage), and banded birds were observed frequently at close range without a detectable signal or visible transmitter. One female Bobolink was observed flying to an area in the hedgerow immediately after release, and the tag was detected there in <1 hr where it remained with no bird present. Several attempts >1 hr were made to retrieve lost tags by tracking signals and searching the vegetation in the area where the signal was strongest but were unsuccessful because of dense vegetation and small transmitter size. No birds were recaptured incidentally in either study to allow examination of the tag attachment site and assess bird health; however, there was no evidence of bird mortality.

DISCUSSION

Although sample sizes for Bobolinks (n = 15) and Chimney Swifts (n = 12) were limited, there was relatively little variation in the retention times within each species, as all the Chimney Swifts retained transmitters long enough for adequate short-term study yet none of the Bobolinks did. Bobolink transmitters were removed before the first relocation (generally within 24 hrs), thus it is not possible to estimate a more precise retention rate. Both species received the same tags and were attached to clipped feather shafts with the same glue, which suggests species-specific differences as the primary explanation for disparity in retention rates, likely related to bill morphology, physical interaction with habitat, and behavior. Bobolinks have strong seed-crushing bills and

spend most of their time in dense ground vegetation where they often preen and forage for seeds and insects (Martin and Gavin 1995), while Chimney Swifts are aerial insectivores with smaller, weaker bills and fly almost continuously except when at their nests and while roosting (Cink and Collins 2002). Tag loss in Bobolinks can therefore be caused both by damage or removal by the bird or by stress put on the attachment point by friction between the tag and vegetation. However, the latter seems very unlikely for Chimney Swifts based on our observations, because the swifts rarely come into contact with vegetation, the main stress on transmitter attachments would be from removal attempts by the birds themselves. The high retention rate for Chimney Swifts indicates that either the birds are not bothered by the transmitters, or they lack the beak strength to remove them.

We determined that attaching radio-transmitters to clipped feathers with glue is an adequate method to monitor Chimney Swifts with radiotelemetry for short-term study and thus should be preferred for this species over other methods for small birds, such as harnesses, which generally pose greater risk to the wearer (Sutherland et al. 2004), particularly for a bird continually in flight. However, the minimal duration of retention we estimated for Bobolinks indicates that glue-attachment methods cannot be universally applied across species. We also noted that at least two Bobolinks (13% of our sample) did not lose their transmitters altogether, but disabled or removed the antenna, which is a problem that attachment method alone is unlikely to fix. For Bobolinks, the minimal duration of retention is likely the consequence of their behavioral traits and their ability to remove transmitters with their strong beaks. This may indicate that using cotton fabric to increase surface area, as we did for Chimney Swifts, likely would not have improved retention success on Bobolinks. Numerous studies have attached tags directly to feathers or skin (49%; Table 1) and many have demonstrated comparable retention success to those that used a fabric interface. Thus, the complete tag loss or damage we observed from Bobolinks would render any plausible benefit from the addition of fabric to be inconsequential. The retention rate for Chimney Swifts compares favorably to a study on Vaux's Swifts (*Chaetura vauxi*) where transmitters without fabric glued to a bare spot trimmed on the interscapular region remained for 2–4 weeks (Bull and Blumton 1997). Our observations of Bobolinks were similar to those of Johnson et al. (1991) using this method, though with fabric, on Northern Cardinals (*Cardinalis cardinalis*) and Blue Jays (*Cyanocitta cristata*) (Table 1), where almost all tags recovered were damaged and most were completely removed by Northern Cardinals within days of attachment (mean = 5 days, n = 16).

Alternative methods, such as a non-permanent weak-link leg harness (tested on Tuamotu Kingfishers, *Todiramphus gambieri*; Kesler 2011), combined with gluing or tying the antenna to tail feathers, may be helpful for such species with low probabilities of retaining glue-attached tags. Woolnough et al. (2004; Table 1) found that glue-attached tags initiated more of a pecking response and had reduced retention because of removal compared to a Rappole harness (Rappole and Tipton 1991) on European Starlings (*Sturnus vulgaris*). Tags for species such as Bobolink can be damaged or destroyed without complete removal, and thus need design modifications to reduce or prevent these risks. Stronger, shorter antennas with reinforced bases in combination with hardier temporary attachment methods may allow short-term telemetry studies on species that damage or remove glue-attached tags while still avoiding higher-risk attachment methods (Barron et al. 2010). Development of shorter antennas with comparable detection may be especially important for ground-foraging birds that may be more likely than others to experience transmitter loss or entanglement (Hill and Elphick 2011). Stronger antennas will inevitably increase overall transmitter weight. Researchers should inquire about possible modifications to standard models if they suspect their study subjects may damage the transmitter in removal efforts, as reinforcement options are now available from some suppliers.

Licensed banders (with telemetry authorization) attempted to radio-track birds (Hill and Elphick 2011) and revealed that 33% of species (n = 63) removed and 29% damaged at least one transmitter attached with glue or harness. However, because of the nature of the survey, they did not identify species that experienced tag loss or indicate if pervasive tag loss resulted in project failure, and only one instance reported is documented in the literature (though could not be identified) which highlights the extent to which these issues are underrepresented in the literature, particularly for passerines (Barron et al. 2010).

Problematic species, guilds, or particular bird attributes need to be identified (Hill and Elphick 2011), and the relative efficiency of specific attachment methods and transmitter modifications needs to be examined. The many variations to glue-attached methods (Table 1) such as the type of glue, whether a fabric interface is used, and if transmitters are glued to skin, clipped, or unclipped feathers, to the middle or lower back, make it difficult to identify trends or generalizations in method performance. As well, data collection methods and retention rate reporting are quite variable. The effect of species appears to be most important from the drastically contrasting success of various specific attachment methods on different species, and researchers should consult examples of telemetry studies on species that have the most similar traits to their chosen study species.

We have shown that species such as Chimney Swift, which have weak bill morphology and little interaction with physical habitat, can safely be monitored for several weeks with radio-transmitters affixed with cyanoacrylate glue. However, species such as Bobolink, grassland birds with strong seed-crushing bills, need a different approach to tag-attachment and a tag that can withstand damage inflicted by the bird. We encourage future studies to report assessments of attachment methods in the literature and support the development of other mediums for recording experiences, such as online forums or databases (Hill and Elphick 2011), to continue to increase the efficiency and improve the efficacy of radio-transmitter based research.

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RELATIVE ABUNDANCE OF SMALL MAMMALS IN NEST CORE AREAS AND BURNED WINTERING AREAS OF MEXICAN SPOTTED OWLS IN THE SACRAMENTO MOUNTAINS, NEW MEXICO

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ABSTRACT.—Mexican Spotted Owls (*Strix occidentalis lucida*) are common in older forests within their range but also persist in many areas burned by wildfire and may selectively forage in these areas. One hypothesis explaining this pattern postulates that prey abundance increases in burned areas following wildfire. We observed movement to wintering areas within areas burned by wildfire by four radio-marked Mexican Spotted Owls in the Sacramento Mountains, New Mexico. These movements occurred during the winters of 2004–2005 and 2005–2006, with some owls migrating in both winters and others in only one. Wintering areas of these owls occurred within the perimeters of two wildfires that burned in May 2000 and April 2002, respectively. We estimated relative prey abundance and biomass during December 2006 within paired burned wintering areas and nest core areas used by these owls. Species richness and relative abundance of small mammals were greater in the burned wintering areas than in the associated nest core areas for all four owls, and estimated prey biomass ranged from 2–6 times greater in burned wintering areas relative to the paired nest core areas. Burned wintering areas used by these owls were similar in elevation to their nest core areas, and likely experienced similar weather conditions during winter. These results suggest that wintering owls moved to areas with greater food resources, rather than to areas with milder weather. They further suggest that relative prey abundance was greater in burned wintering areas than in the nest core areas >5 years post-fire, and that these burned wintering areas provided important habitat for Mexican Spotted Owls in our study area during an energetically stressful season. *Received 29 July 2013. Accepted 2 November 2013.*

Key words: Mexican woodrat, migration, prey abundance, prey biomass, species richness, voles, wildfire effects.

The Mexican Spotted Owl (*Strix occidentalis lucida*) occurs in canyonlands and forested mountains throughout the southwestern United States and the Republic of Mexico (Gutiérrez et al. 1995, Ward et al. 1995, U.S. Department of the Interior 2012). It frequently occupies older forests or forests with late-seral characteristics (Ganey and Dick 1995, U.S. Department of the Interior 2012), and was listed as Threatened under the Endangered Species Act in 1993, primarily because of concerns over the loss of older forest habitat to timber harvest (U.S. Department of the Interior 1993). Since that time, a number of large wildfires have burned within the range of the Mexican Spotted Owl, and many of these fires have impacted areas that were known to be occupied by Spotted Owls. As a result, wildfire has now supplanted timber harvest as the greatest perceived threat to the owl and its habitat (U.S. Department of the Interior 2012). Thus, understanding the impact of wildfires on population dynamics and habitat use of Mexican Spotted Owls is an area of growing interest (U.S. Department of the Interior 2012).

Wildfire can alter structure in or eliminate the older forests used by Mexican Spotted Owls over large areas, leading many observers to assume that wildfires routinely result in complete loss of habitat for Mexican Spotted Owls (e.g., Sheppard and Farnsworth 1995). However, available evidence suggests that these owls often persist in burned areas, at least in the short term (Bond et al. 2002; Jenness et al. 2004). Similar evidence exists for the California Spotted Owl (*S. o. occidentalis*; Bond et al. 2002, 2009, 2010, 2013; Roberts et al. 2011; Lee et al. 2012), and California Spotted Owls have been observed to selectively forage in burned areas (Bond et al. 2009).

One potential explanation for the continued use of burned areas by Mexican Spotted Owls postulates that abundance of the small mammals that dominate their diet (Ganey 1992, Ward and Block 1995, Seamans and Gutiérrez 1999, Block

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et al. 2005) may increase following fire, at least in the short term, and that owls thus may find favorable foraging habitat in burned areas (Bond et al. 2002, 2009, 2010; US Department of the Interior 2012). Studies within the range of Mexican Spotted Owls suggested increases in some species of small mammals following wildfire (Kyle and Block 2000, Converse et al. 2006), but data on this subject generally are sparse and short term. Thus, it is unknown whether or not increased prey abundance following fire is a general pattern, or how long such increases persist if they do occur.

In conjunction with a study on demography of Mexican Spotted Owls in the Sacramento Mountains, New Mexico, we observed movement by four radio-marked owls during winter from nest core areas in closed-canopy mixed-conifer forests to areas burned in two large wildfires. Because winter is suspected to be a time of food shortage for Mexican Spotted Owls (Block et al. 2005, Ganey et al. 2005) and prey abundance is hypothesized to increase post-fire, these moves might indicate a shift to areas of richer food resources. We examined species richness, relative abundance, and biomass of prey at potential foraging areas around winter roost sites for owls within the burned wintering areas and at paired nest core areas used by these owls. Thus, we provide data on potential differences between burned wintering areas and nesting areas in prey abundance and biomass during an energetically stressful season for Spotted Owls.

STUDY AREA

Our study area was approximately 50,000 ha in the Sacramento Mountains, south-central New Mexico, USA. This area encompassed much of the central portion of the Sacramento Ranger District, Lincoln National Forest, including the village of Cloudcroft, New Mexico. Elevation ranged from 2,000–2,800 m. Terrain consisted of heavily forested montane slopes and minor tributaries, with interspersed meadows in the larger valley bottoms. The predominant forest type was mixed-conifer, singularly or co-dominated by white fir (*Abies concolor*) and Douglas-fir (*Pseudotsuga menziesii*). Other common tree species included southwestern white pine (*Pinus strobiformis*), ponderosa pine (*P. ponderosa*), and quaking aspen (*Populus tremuloides*) (Kaufmann et al. 1998, Ward 2001). Precipitation averaged 65 cm/yr at Cloudcroft (2,652 m) with summer thunderstorms providing more than 60% of annual precipitation and most of the remainder occurring as winter snowfall (Kaufmann et al. 1998).

Two large wildfires burned within this study area in 2000 and 2002. The Scott Able fire ignited on 11 May 2000, and burned 6,213 ha, with approximately 16 and 25% of this area burned at moderate and high severity, respectively (Monitoring Trends in Burn Severity 2013). The Peñasco fire ignited on 30 April, 2002, and burned 6,073 ha, with approximately 29 and 17% of this area burned at moderate and high severity, respectively (Monitoring Trends in Burn Severity 2013).

METHODS

We located general areas occupied by Mexican Spotted Owls within the study area using nocturnal calling surveys (Forsman 1983). We captured owls during daytime follow-up surveys, using snare poles and baited mist nets, and attached radio transmitters using a backpack harness constructed of Teflon ribbon. All owls discussed here were captured during the summers of 2004 or 2005, and were radio-tracked though fall 2006. Radio-marked owls were not located frequently during the winter months because of constraints in funding and personnel availability, as well as access issues. Most locations recorded for Mexican Spotted Owls were from visual observations obtained during the day. Consequently, we defined movement to a wintering area as occurring when a radio-marked owl was located roosting during the day in an area >2 km from their nest/roost core (after Ganey and Block 2005) on multiple occasions between 1 November–15 April, with the roost locations separated by <300 m and occurring over a period of >18 days.

Five radio-marked owls satisfied these criteria, with four of these owls using areas burned by wildfires. We established two trapping grids for each of these four radio-marked owls. One grid was established within their nest core area (see below) and the second within their burned wintering area. We used the nest core area for comparative purposes, because these areas represented activity centers used during the breeding season and available foraging habitat which these owls, by moving to geographically distinct wintering areas, were not selecting. All nest core and burned wintering areas were located within the same forest cover type (mixed-conifer forest).

TABLE 1. Summary of migratory movements observed during the winter by five radio-marked Mexican Spotted Owls in the Sacramento Mountains, New Mexico, 2004–2006.

Owl territory	Owl sex	Fire area used	Winters in which owl migrated to winter area	Years post-fire	Distance from nest to winter area (km)	Elevation difference (m)[a]
010	M	Scott Able	2004–2005	4+	2.1	0
027	F[b]	Scott Able	2004–2005	4+	12.0	0
027	M[b]	Peñasco	2004–2005, 2005–2006	2–3+	7.1	180
104	F	Scott Able	2004–2005, 2005–2006	4–5+	14.0	35
067	F	NA[c]	2005–2006	NA	9.8	600

[a] Elevation difference computed as nest elevation – burned wintering area elevation.
[b] Burned wintering areas used by these mated owls were separated from each other by 8.3 km.
[c] This wintering area was not included within a fire perimeter. We considered this an example of altitudinal migration, and did not include nest core or wintering areas of this owl in small mammal trapping operations.

Nest core areas (40-ha each) were defined following Ward and Salas (2000). Wintering areas were defined by placing a 200-m buffer around all observed roost locations for each owl using Arcview 3.2 (ESRI Inc. 1999) then merging these buffers to create a single unique polygon for each owl. The 200-m buffers used were arbitrary, but were intended to define an area close to the observed roost sites and therefore readily available for foraging owls. We observed these owls foraging near their roosts during the day on several occasions.

Trapping grids were established at a randomly generated location in both nest core and burned wintering areas. At each grid location, we set 20 traps in two parallel lines (10 traps/line), with 20-m spacing between traps. We placed 1 extra-large (10 × 18 × 60 cm) Sherman live trap at each trap station. We baited traps with a mixture of peanut butter, rolled oats, and bird seed, supplied abundant cotton batting in traps to provide bedding material for captured animals during cold winter nights, and covered traps with 1–3 cedar shingles to provide additional insulation.

We trapped all grids over a 2-week period from 4–15 December 2006. We checked traps in each grid each morning for 4 days (n = 80 potential trap nights/grid). We noted any cases where traps were sprung without capturing an animal and subtracted such traps from available trap occasions. We marked each animal captured with a single numbered ear tag (Monel-1005s1, National Band and Tag, Newport, Kentucky), to allow identification of new versus recaptured individuals, and recorded species (or genus for white-footed mice [*Peromyscus* spp.]) of the captured animal. All captured animals were released unharmed at the point of capture.

For each transect, we report the number of unique individuals captured by species and total biomass of all species. We used the number of unique individuals captured as an index of abundance, because this index often outperforms model-based estimators of abundance when data are sparse (McKelvey and Pearson 2001). Biomass (g) was calculated as the summed biomass of all unique individuals captured. We used values presented in Ward (2001; Table 2.8) to generate mass estimates for individual prey species. Ward (2001; Table 2.8) presented means for small mammals trapped in each of four cover types in the Sacramento Mountains. We averaged these mean values across the four cover types to generate our mass estimates. Because capture data were sparse, we did not conduct formal statistical analyses and simply present summary information here.

RESULTS

Five radio-marked owls from four unique owl territories moved from their breeding area to geographically distinct wintering areas, based on our movement criteria (Table 1). One owl moved to a wintering area 600 m lower in elevation than the nest core area and located outside of the fire perimeters. We considered this an example of altitudinal migration (Ganey and Block 2005) and did not trap small mammals in this wintering area.

Only two species of small mammals (white-footed mice and Mexican woodrats [*Neotoma mexicana*]) were captured in nest core areas, with white-footed mice accounting for 85% of individuals captured (Table 2). In contrast, four species were captured in burned wintering areas (white-footed mice [72% of individuals captured], Mexican woodrats, and both long-tailed [*Microtus*

TABLE 2. Numbers of small mammals captured by species and estimated biomass of small mammals trapped in nest core and burned wintering areas used by four radio-marked Mexican Spotted Owls in the Sacramento Mountains, New Mexico, 2004–2006.

				Number of unique individuals captured				
Territory	Owl sex	Grid type	Trap occasions[a]	White-footed mouse	Mexican woodrat	Long tailed vole	Mogollon vole	Biomass (g)[b]
010	M	Nest core	78	4	2	0	0	306.8
		Winter area	74	4	4	1	0	577.9
027	F[c]	Nest core	76	5	0	0	0	86.0
		Winter area	75	18	1	0	3	507.2
027	M[c]	Nest core	76	5	0	0	0	86.0
		Winter area	72	4	1	0	0	187.8
104	F	Nest core	73	2	0	0	0	34.4
		Winter area	77	11	0	0	0	189.2

[a] Calculated as (number of traps ×4 occasions) minus number of sprung or otherwise unavailable traps.
[b] Biomass estimates used were derived by averaging estimates from Ward (2001: table 2.8) across four cover types. Estimates used here were: white-footed mouse = 17.2 g, Mexican woodrat = 119.0 g, long tailed vole = 33.1 g, and Mogollon vole = 26.2 g
[c] The same nest core area was used for both the male and female from territory 027.

longicaudus] and Mogollon [*M. mogollonensis*] voles; Table 2).

Relative prey abundance in winter was low in all areas, but was greater in burned wintering areas than in the paired nest core areas (Table 2). In addition, estimated prey biomass ranged from approximately double to almost six times greater in burned wintering areas relative to the paired nest core areas. Total biomass of individuals captured in burned wintering areas was 237.2 g greater than biomass captured in nest core areas, on average (95% CI = 12.0–462.5 g), despite having more trap occasions in the nest core area in three of four cases (Table 2).

DISCUSSION

Our results support the hypothesis that prey resources were greater in the burned wintering areas than in the paired nest core areas. Species richness, relative abundance, and biomass of small mammals during the trapping period all were greater within the burned wintering areas than within the paired nest cores of the radio-marked owls. Because the Scott Able fire burned in May 2000 and we trapped small mammals in that area during December 2006, our results suggest that prey abundance in the burned wintering areas was greater than in the nest core areas even where those burned wintering areas were >6 years post-fire.

Although many radio-marked Mexican Spotted Owls in previous studies remained in their breeding areas during winter, some individuals in all populations studied migrated to wintering areas at lower elevations (Ganey and Block 2005: Table 2). Such movements typically allowed migrating owls to winter in areas featuring warmer temperatures below the level of persistent snow, but also could be driven by relative prey availability. Only one study (Block et al. 2005), involving two radio-marked owls from a single territory, quantified differences in prey abundance between lower elevation wintering areas and nest core areas. These owls moved ~40 km from their nesting area in ponderosa pine – Gambel oak (*Quercus gambelii*) forest to a wintering area in pinyon (*Pinus* spp.) – juniper (*Juniperus* spp.) woodland, ~920 m lower in elevation than the nest area. Prey biomass during the winter was approximately seven times greater in the wintering area than in the nesting area of these owls (Block et al. 2005). Thus, these owls moved a relatively long distance to a wintering area at lower elevation in a completely different forest cover type, which featured both milder weather and higher prey abundance.

In contrast, the burned wintering areas used by owls in our study were similar in elevation to the paired nest core areas, <15 km from those nest core areas in all cases, and located in the same forest cover type. Consequently, these owls did not appear to be moving to areas with more favorable weather conditions, such as warmer temperatures or reduced snow cover. The fact that they moved to areas with richer food resources suggests that they may have been seeking greater prey abundance during a season when prey for Mexican Spotted Owls are suspected to be scarce

(Ward 2001, Block et al. 2005, Ganey et al. 2005). Bond et al. (2010) also documented expanded winter movements and use of burned areas by radio-marked California Spotted Owls, and Irwin et al. (2013) documented preferential use of harvested areas by Northern Spotted Owls (*S. o. caurina*) during winter. Irwin et al. (2013) suggested that such use may have been a response to greater prey abundance in these areas.

Clearly, our data were sparse, and involved a limited trapping effort in one time period and in burned wintering and nest core areas of only four owls. We were not able to estimate detection probabilities, and so cannot rule out the possibility that trappability of small mammals differed between nest cores and burned wintering areas, although we have no biological reason to suspect such a difference. We also were not able to generate estimates of precision around abundance estimates, which limits the strength of our comparisons between paired nest core and burned wintering areas (McKelvey and Pearson 2001). The observed differences between paired nest core and burned wintering areas were both relatively large and consistent in direction, and the index of abundance that we used has been shown to perform well in many situations (McKelvey and Pearson 2001).

Finally, because our study was opportunistic and observational rather than experimental, we cannot conclusively attribute differences in prey abundance between paired nest core and burned wintering areas to the effects of wildfire. Paired nest and burned wintering areas sampled were separated in all cases by <15 km, and were similar in elevation and located in the same forest cover type. Thus, the primary difference between these paired areas was that wintering areas were burned and nest cores were not. Consequently, it seems likely that fire effects at least partly explained the observed differences in prey abundance between these paired sites.

It would be desirable to confirm our results with additional and more intensive trapping over longer time frames and on more than one occasion, in multiple seasons, and in more geographic areas throughout the range of Mexican Spotted Owls. In the meantime, however, our results suggest that the burned wintering areas used supported greater species richness, relative abundance, and biomass of prey than the paired nest core areas, that these differences were observed as much as >6 yrs post-fire, and that in our study area these burned wintering areas provided important habitat for Mexican Spotted Owls during an energetically stressful time of year.

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HOME RANGE CHARACTERISTICS OF MEXICAN SPOTTED OWLS IN THE RINCON MOUNTAINS, ARIZONA

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ABSTRACT.—We studied a small isolated population of Mexican Spotted Owls (*Strix occidentalis lucida*) from 1996–1997 in the Rincon Mountains of Saguaro National Park, southeastern Arizona, USA. All mixed-conifer and pine-oak forest patches in the park were surveyed for Spotted Owls, and we located, captured, and radio-tagged 10 adult birds representing five mated pairs. Using radio-telemetry, we examined owl home range characteristics, roost habitat, and monitored reproduction within these five territories. Breeding season (Mar–Sep) home range size for 10 adult owls (95% adaptive kernel isopleths) averaged 267 ha (±207 SD), and varied widely among owls (range 34–652 ha). Mean home range size for owl pairs was 478 ha (±417 ha SD), and ranged from 70–1,160 ha. Owls that produced young used smaller home ranges than owls that had no young. Six habitat variables differed significantly between roost and random sites, including: percent canopy cover, number of trees, number of vegetation layers, average height of trees, average diameter of trees, and tree basal area. Radio-marked owls remained in their territories following small prescribed management fires within those territories, exhibiting no proximate effects to the presence of prescribed fire. *Received 11 February 2013. Accepted 9 November 2013.*

Key words: Arizona, habitat, home range, Mexican Spotted Owl, Rincon Mountains, Saguaro National Park, *Strix occidentalis lucida*.

The Mexican Spotted Owl (*Strix occidentalis lucida*) is distributed among forest highlands and rocky canyonlands in the southwestern United States and Mexico (U.S. Department of the Interior 2012). Mexican Spotted Owls were listed as "threatened" by the U.S. Fish and Wildlife Service in 1993 because of perceived threats from timber harvest and wildfire (Cully and Austin 1993). This subspecies is strongly associated with older forests and forests with complex structure (Ganey et al. 1999), and habitats used by Mexican Spotted Owls vary by region (Rinkevich and Gutiérrez 1996, Ganey et al. 2005, Willey and van Riper 2007, Mullet and Ward 2010).

In this study, we examined home range size and roosting habitat of a small, relatively isolated population of Mexican Spotted Owls in the Rincon Mountains, southeastern Arizona (Fig. 1). The Rincons are part of the Madrean Sky Island archipelago (Boyd 2002), a chain of isolated highlands with high-elevation coniferous forests frequently occupied by Spotted Owls (Danzer 2005). Home range size of Mexican Spotted Owls varies widely among regions and habitat types, and information is lacking for many areas, including the Sky Island ranges of southeast Arizona (Ganey and Dick 1995, U.S. Department of the Interior 2012). Our primary objectives were to: (1) survey high-elevation forests in the Rincons to locate and capture Mexican Spotted Owls, (2) estimate home range size and describe home range characteristics of radio-marked owls, and (3) describe habitat characteristics of nest and roost sites used by the owls. In addition, several prescribed burns were conducted within owl territories during this period, providing an opportunity to observe potential impacts of these fires.

METHODS

Study Area.—The Rincon Mountains are located approximately 12 km east of Tucson, Arizona (Fig. 1), and are largely contained within the eastern district of Saguaro National Park. The Rincons encompass 25,000 ha of roadless area ranging in elevation from 1,988–2,599 m. Mexican Spotted Owls inhabit conifer forests within the upper elevations of the Rincons. These conifer forests included two vegetation series (Brown 1982), one composed of ponderosa pine (*Pinus ponderosa*), southwestern white pine (*P. strobiformis*), and several oaks (mostly *Quercus gambelii, Q. hypoleucoides*, and *Q. arizonica*) on south-facing slopes; and a mixed-conifer series, that included Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), ponderosa pine, and southwestern white pine on north-facing slopes. A variety of grasses, herbaceous species,

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FIG. 1. Location of the Rincon Mountains study area in southeastern Arizona, where Mexican Spotted Owls were studied during 1996–1997, Arizona, USA.

and western brackenfern (*Pteridium aquilinum*) were typically present as understory in both vegetation series.

Surveys and Radio-telemetry.—We conducted night-time calling surveys to locate Spotted Owls during May–July 1996 using a standardized procedure (Forsman 1983). We systematically surveyed all forests using routes established along an existing, and extensive, trail network in the park. After owls were detected at night, we conducted daytime visits to locate roosting birds, find nests, and count fledgling owls. We captured owls using Bal-Chatri traps and noose poles (Willey and van Riper 2007). We installed a 5-g tail-mounted radio-transmitter (Model RA-1, Holohil Systems, Ltd., Ontario, Canada) with an average signal life of 12 months. We used TR-2 receivers and handheld antennas (Telonics Inc., Mesa, Arizona, USA) to estimate owl locations for home range estimates. Nocturnal tracking was conducted by a 3-person team during May–September in both 1996 and 1997. We established permanent tracking stations at high points across our study area from which owl locations were estimated by simultaneous intersection of compass bearings from three stations. Our nocturnal tracking schedule was designed to track a focal pair of owls one night per week using a 5-hr tracking session per night. We alternated between an early period (sunset to midnight) and late period (midnight to sunrise) for each owl pair. During each session, we attempted to secure at least one location per owl per period and attempted to keep sampling equal among owls. However, for various reasons, including weather and transmitter failures, this was not possible. In addition, daytime tracking was conducted in each owl territory twice per week to locate roost sites and assess nesting status.

Home Range Estimation.—We estimated errors associated with radio-tracking by taking test triangulations from tracking stations. We estimated the location of test transmitters with the observer naïve to actual transmitter locations

(White and Garrott 1990). We then calculated the mean and standard deviation of bearing errors. Owl locations, and error polygons, were estimated using the maximum likelihood Lenth estimator (Lenth 1981), as modified by Lee et al. (1985). We defined the breeding season as March–September (U.S. Department of the Interior 1995), and estimated cumulative breeding season home range size for each radio-tagged owl as the union of the seasonal ranges from 1996 and 1997 using only nighttime locations (i.e., we did not use roost or nest sites in the home range analysis). We calculated 95% AK estimates and used the least-squares cross-validation method to guide selection of a smoothing parameter (Seaman and Powell 1996, Willey and van Riper 2007, Bowden 2008). To identify areas of concentrated use within a home range, we generated 75% AK isopleths (U.S. Department of the Interior 1995, Willey and van Riper 2007). We generated home range models using program LOAS 4.0a (Ecological Software Solutions LLC, Florida, USA) and ArcView 3.2 (ESRI, Redlands, CA). We calculated mean home range size and associated standard errors (SE) for AK95% and AK75% isopleths for individual owls and pairs combined. Finally, we used a correlation analysis to inspect relationships between the number of telemetry locations and size of home range isopleths (Zar 1999). Autocorrelation may be a concern with home range estimation where statistical models assume locations are independent (Swihart and Slade 1986); however, the minimum time we allowed between telemetry locations (>1 hr) was sufficient to allow a focal owl to traverse its entire home range, thus our approach provided biological independence and reduced incidence of autocorrelation (Otis and White 1999).

Spotted Owl Habitat Use.—We located roost sites of Mexican Spotted Owls during the day and measured variables in habitat plots centered on roosts. We also established 30 random plots located within 500 m of each primary roost area (n = 150 random plots) to describe available habitat within an area that typically contained territorial activity centers, included roost and nest sites, and primary foraging areas (U.S. Department of the Interior 1995). Our goal was to describe habitat use versus availability within the activity center of home ranges (U.S. Department of the Interior 1995); therefore, we selected random habitat plots within a 500-m radius centered on the nests or primary roost locations within each mated pair home range. Points were drawn randomly from Universal Trans Mercator (UTM) grid intersections (i.e., 100 × 100 meter pixels) within the buffered area, and located in the field using a global positioning device. Vegetation and physical habitat variables were recorded within 0.04-ha plots centered at each habitat sample-point following methods described by Willey (1998). Measured habitat variables included: the number of vegetation layers present; tree species composition; and individual tree dimensions including tree height (m), diameter at breast height (cm), basal area factor (using a wedge prism), and percent canopy cover (calculated from data derived with a spherical densiometer). Several abiotic features were also measured, including: percent slope (clinometer), slope aspect (compass), elevation (altimeter), and plot temperature (Celsius thermometer measured at ground level, plot center). We measured roost and random plot temperature for each pair during the same afternoon during 1,200–1,500 hrs when summer temperatures typically reached their zenith. We calculated the mean angle of orientation of roost sites, and tested for nonrandom compass orientation of roosts following procedures outlined by Batshelet (1981). We contrasted roost versus random habitat plots using the nonparametric two-sample Mann Whitney U-test. Statistical significance was set for all tests as $P \leq 0.05$ (Zar 1999).

RESULTS

Spotted Owl Surveys.—We located and radio-marked five pairs of owls during our surveys in the Rincon Mountains during April–July 1996 (Table 1). Only the Reef Rock pair (hereafter, REEF) successfully produced juveniles (n = 2) during 1996. During 1997, one territory (ITALY) produced two juveniles. The successful REEF nest site was in a large Gambel's oak cavity, while the ITALY nest was on a mistletoe platform in a mature Douglas-fir tree. Fledgling Spotted Owls in the REEF and ITALY territories were observed each week, starting in mid-July, until they dispersed from natal areas during mid-September both years, and fledglings remained within 300 m of nest sites until dispersal. Although no juvenile owls were detected in the other territories, we did observe courtship behavior at those sites, and suspect that nesting was attempted but failed for unknown reasons.

TABLE 1. Home range information, including number of telemetry locations, tracking-period, and adaptive kernel (AK) home range estimates for 10 radio-tagged Mexican Spotted Owls representing five mated pairs in the Rincon Mountains, Arizona, 1996–1997. We used the AK95% and AK75% isopleths to estimate home range and activity center size, respectively. Both individual and pair range estimates are shown.

Owl code	Number locations	Tracking period	AK95% size (ha)	AK75% size (ha)
ITALY Pair	67	April 1996–October 1997	70	5
Male	20	April–November 1996	34	4
Female	47	April 1996–October 1997	53	7
HELEN Pair	112	April 1996–October 1997	249	88
Male	46	April 1996–October 1997	221	74
Female	66	April– November 1996	116	60
REEF Pair	64	April–October 1996	374	46
Male	28	June–October 1996	124	56
Female	36	April–June 1996	176	54
SPUD Pair	242	April 1996–September 1997	537	161
Male	124	April–October 1996	398	128
Female	118	September 1996–September 1997	473	169
RINCON Pair	88	May–October 1996	1160	305
Male	32	May–October 1996	652	205
Female	56	May–September 1996	425	211

Home Range Characteristics.—The mean bearing error in radio-telemetry test triangulations was 2.5° (±10° SD, n = 150 test triangulations), and the mean area of confidence ellipses derived for all owl locations (n = 2,123) was 5 ha (±4 ha SD). To reduce spatial error, we used only those owl locations with error ellipses ≤5.0 ha (n = 573) for home range estimates. The mean size of AK95% isopleths was 267 ha (±207 SD) and ranged from 34–652 ha among the owls (Table 1). Mean size of pair AK95% ranges was 478 ha (±417 ha SD) but varied among the owls (Table 1). Owl pairs that produced young appeared to use smaller activity centers within home ranges (mean AK75% = 26, SE = 21) than owls that had no young (mean AK75% = 185, SE = 64), but statistical power to detect differences based on breeding status was low because of small sample size.

Patterns of spatial use suggested that radio-marked owls used "activity centers" within the home ranges, for example, AK75% isopleths identified areas of concentrated use within each owl's home range, generally surrounding centrally located nest or roost sites. Activity centers averaged 97 ha (±78 SD) in area, and variability in activity center size was lower among owls than variability in home range size (Table 1). Correlation between the estimated AK95% home range size and number of owl relocations showed a positive relationship (0.41) between number of locations and home range size. However, when the pair (ITALY) with the lowest number of relocations was removed from the analysis, the estimated correlation dropped to 0.27. The correlation between owl pair AK95% home ranges and number of owl relocations was relatively low (0.11), and dropped to 0.09 when the ITALY pair was removed from the analysis.

Roost Habitat.—We located and measured habitat at 53 roost sites among the five owl pairs (Table 2). During both years, most roosts were located on northwest slopes in mixed-conifer forest. The roost analysis showed nonrandom placement of roosts with respect to the random points within home range areas (Batschelet [1981] test, P = 0.49, significantly different from random, $P < 0.005$), where most roosts faced in a northerly direction. On the north-facing mixed-conifer slopes, average roost temperature was significantly cooler than temperatures measured at random sites (two-sample t-test, $P < 0.05$), with the average difference between roost and random equal to 15 °C (Table 2).

Roosts of Mexican Spotted Owls were located in the following tree species: Douglas-fir, ponderosa pine, New Mexico locust (*Robinia neomexicana*), Gambel oak and southwestern white pine. One roost was located in a pine snag. Ninety-three percent of roost plots were dominated by mixed-conifer forest, 7% by pinyon-juniper woodland, and no roosts were located in pine-oak forest.

TABLE 2. Roost site characteristics (n = 53 roosts) measured within 5-m of roosts for 10 Mexican Spotted Owls in the Rincon Mountains, May–August 1996, Arizona.

Variable	Range	Mean value
Aspect	0–360°	338° (r = 0.117, s = 111)[1]
Slope	0–28.3°	25.2°
Elevation	2,288–2,587 m	2,476 m
Roost temperature	−1.1–29.4 °C	17.3 °C
Ambient temperature	1.7–33.3 °C	20.2 °C

[1] r = mean vector, and s = angular variation (Batschelet 1981).

Elevation of roost plots differed among owl territories (ANOVA, F = 16.75, P < 0.05, df = 119), but no roosts were found below 2,140 m. Six habitat variables differed significantly between roost sites and random sites, including: percent canopy cover, number of trees, number of vegetation layers, average height of trees, average diameter at breast-height, and tree basal area (Table 3).

TABLE 3. Contrast of habitat features at 150 random habitat plots and 53 roost plots of Spotted Owls in the Rincon Mountains, Saguaro National Park.

Variables	Median value		P-value
	Roost	Random	
Canopy cover (%)	96.5	89.8	0.009*
Vegetation layers	2.0	3.0	0.049*
Slope (degrees)	22.5	19.5	0.163
No. snags	0.5	1.0	0.917
No. trees	6.5	4.0	0.001*
No. tree species	2.0	2.0	0.419
Tree height (m)	12.5	10.0	0.012*
Tree diameter (cm)	33.0	23.0	0.008*
Basal Area Factor	14.0	12.0	0.024*

* Significantly different, $P \leq 0.05$, Mann Whitney U-test.

DISCUSSION

Breeding season home range size of Mexican Spotted Owls in the Rincon Mountains was highly variable, for example, the size of AK95% isopleths ranged from 34–652 ha among individual owls (Table 1). Although the overall mean home range area was 268 ha (SE = 66), one pair of owls (i.e., ITALY) showed unusually small home ranges (≤53 ha). A correlation analysis showed a strongly positive association (0.41) between range size and number of owl relocations, and with ITALY removed from the analysis, the correlation dropped to 0.27, and average home range size increased to 323 ha (SE = 68). The average home range size for mated pairs (478 ha, SE 187) was somewhat larger than for individuals within the pairs, suggesting that males and females used certain distinct portions of the landscape. In addition, the RINCON pair was located 8 km south of the other owls, and used a relatively large area (1,160 ha) compared to the other pairs (mean = 387 ha with ITALY removed) located on Mica Mountain. Although home ranges did not overlap on Mica Mountain, on average, those territories were less than half the size of the isolated RINCON pair.

Home range size for this species varies considerably by region (Ganey et al. 1999, Forsman et al. 2005, U.S. Department of the Interior 2012). For the Rincons, we observed home ranges were typically smaller than those reported for Mexican Spotted Owls in other areas. Our correlation analysis, and subsequent inspection of estimated home range sizes, indicated that a low sample of relocations for the ITALY pair likely biased our estimates. With that pair removed from the analysis, mean size increased but remained lower than most estimates from other regions. In forests of northern Arizona, Ganey et al. (1999) reported mean size of 895 ha, and Zwank et al. (1994) found cumulative home range size in New Mexico averaged 365 ha. In rocky canyon environments in Utah, cumulative home range size averaged 928 ha (Willey and van Riper 2007), and in similar habitat in the Grand Canyon, Arizona, Bowden (2008) estimated home range size averaged 562 ha. The largest home ranges were reported for the Northern Spotted Owl (*S. o. caurina*) in Washington, where size averaged 4,972 ha (Forsman et al. 2005). Given the variability in methodology for estimating home range size, we urge caution when contrasting results from various regions.

Home range size for Spotted Owls appears to be associated with various factors, including elevation and region (Ganey et al. 2005), habitat complexity and microclimate (Willey 1998, Willey and van Riper 2007, Bowden 2008), and distribution of mature forest and abundance of prey (Carey et al. 1990). In New Mexico, Ganey et al. (2005) documented a strong relationship between home range size and the amount of mixed-conifer forest present. In our study area, forests occurred at the upper elevations and were limited in distribution. The relatively small, isolated forest patches may have affected home range size, but low sample size was also a likely factor in our results. Further

research investigating the distribution and abundance of prey and characteristics of suitable nesting habitat in the relatively restricted space might help illuminate factors that influenced home range size in the Rincons.

Our results concerning roost habitat used by Spotted Owls showed that roost areas were strongly associated with relatively cool north-facing mixed-conifer forests (Tables 2–3). When compared to available habitat, Spotted Owls' roost sites showed relatively high canopy cover, greater number of trees (thus, dense stand structure), larger diameter and taller trees, and a greater number of vegetation layers than measured at adjacent random plots. These relatively dense groves of mixed-conifer forest surrounding roosts provide thermal protection, cover from potential predators, and protected post-fledging areas for juvenile owls (U.S. Department of the Interior 2012). Furthermore, because the roost sites we found were closely associated with nest areas, or locations where we suspect nesting was attempted, our description of roost habitat may help identify important components for nest sites in the study area.

During nighttime telemetry tracking, we often located Spotted Owls in relatively open pine-dominated forests on south-facing slopes, and these locations may have represented places that offered suitable foraging (Ganey 1988, Bowden 2008). Incidental to our study, small prescribed management fires, were conducted each summer on Mica Mountain, and created a mosaic of effects in the pine forests. Following the fires, we continued to locate owls in the burned areas at night during radio-telemetry tracking periods each summer, and all owl pairs were still present the final year of our study. Habitat alteration caused by fire has been identified as a potential threat to Spotted Owls and large wildfires can have catastrophic impacts on forest habitat used by Spotted Owls (U.S. Department of the Interior 2012). We did not observe negative effects on owls as a result of the small prescribed fires or the increased human presence by fire managers. However, potential short- and long-term effects of fire on owls within the limited habitats of the Sky Islands have not been adequately studied, and we recognize the large potential for habitat loss associated with catastrophic fire (Bond et al. 2009, Lee et al. 2012, U.S. Department of the Interior 2012). For the Rincons, a cautious approach to mechanical treatments in mixed-conifer forests, especially where they occur on north-facing slopes where nest and roost areas were concentrated, will benefit Mexican Spotted Owl occupancy and the owl's management throughout the southwestern Sky Islands. We also believe that further investigation concerning the role of fire, habitat structure, prey ecology, and occupancy dynamics of Mexican Spotted Owls throughout the southwestern Sky Islands will benefit conservation management for the owls.

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VINEYARD AND RIPARIAN HABITAT, NOT NEST BOX PRESENCE, ALTER AVIAN COMMUNITY COMPOSITION

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ABSTRACT.—In California, oak woodlands are being converted into vineyards, resulting in a loss of songbird nesting sites. Although many vineyards contain wooded riparian habitat, no previous research has examined the avian species composition in oak-vineyard landscapes. We compared the avian communities associated with vineyard, edge, and riparian habitats and examined to what degree the riparian habitat in vineyard landscapes continues to support birds associated with native oak woodland habitat that spanned the region before agricultural intensification. We further tested whether the presence of nest boxes in vineyard and riparian areas altered avian species composition in the landscape. Mist nets were used to survey the avian community in vineyard, edge, and riparian habitat at four sites during the breeding season. Permutational ANOVAs, using presence-absence data from captures, identified habitat, study sites, and time over the breeding season as highly significant main effects that explained differences in species composition. Establishment of songbird nest boxes did not alter the species composition. Two-thirds of the birds identified as woodland species in prior studies were found in riparian areas adjacent to vineyards, including five watch-list species. Overall the species composition of birds using riparian habitat was greater and significantly different from those found in the vineyard. This highlights the importance of maintaining natural areas like riparian habitat in agricultural landscapes. *Received 10 April 2013. Accepted 24 September 2013.*

Key words: associated diversity, bird nest boxes, boundary effects, conservation, corridor, oak woodlands, riparian buffer, vineyard.

Since 1950, over one million acres of oak woodlands in California have been converted to agricultural or urban land (Merenlender and Crawford 1998, Heaton and Merenlender 2000). The American Bird Conservancy includes California's oak woodlands on their list of the 20 most threatened bird habitats in the United States (ABC 2007), because of rapid conversion of breeding habitat and loss of nesting sites (California Partners in Flight 2002). Because agricultural land-use change is a leading cause of species decline (Sala et al. 2000), agroecological conservation efforts, such as conserving remnant habitat patches and providing artificial nesting sites, need to be analyzed for their effectiveness in providing critical resources for declining populations. Lead by a profitable wine market, vineyard encroachment is still the leading driver in native habitat loss in California's coastal counties (Merenlender 2000). Grapes are the second most important agricultural commodity produced in California, generating over $3.8 billion U.S. dollars in 2011 (California Department of Food and Agriculture 2013), and vineyards span over 847,000 acres across the state (National Agricultural Statistics Service 2013), representing an increasingly important habitat in the landscape.

Although many vineyard landscapes in California contain wooded riparian zones, no previous research has examined whether these remnant riparian habitats are used by native woodland-affiliated avian species. Vineyards are perennial agricultural systems that may incorporate remnant trees, native hedgerows, and low till management practices that conserve soil and water and provide diverse habitats for native flora and fauna (Merenlender and Crawford 1998). In Europe, both woodland and semi-open bird species were shown to be present in vineyards (Verhulst et al. 2004, Laiolo 2005). To our knowledge, the scientific literature contains only two studies that examine avian conservation in North American vineyards. Fiehler et al. (2006) showed that Western Bluebird (*Sialia mexicana*) occupants of nest boxes in California vineyards initiated their nests earlier and produced larger clutches than those occupying nest boxes in adjacent oak woodlands. In the same vineyard sites as this study, Jedlicka et al. (2011) performed avian point

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counts and found insectivorous bird densities in vineyards with nest boxes to be four times greater than in vineyards without nest boxes. Little is known about how birds use agricultural and riparian habitat patches in oak-vineyard landscapes or what factors influence that use. Establishing songbird nest boxes in vineyards has been a popular response by concerned wine grape growers (Heaton et al. 2008), because as oaks and snags are removed, many cavity-nesting songbirds are left without nesting sites (CalPIF 2002). However, it remains unclear whether the provision of songbird nest boxes in riparian areas and neighboring vineyards enhances species diversity along with increasing the abundance of cavity-nesting species.

In this study, we examined to what degree the riparian remnant habitat in vineyard landscapes continues to support birds affiliated with oak woodlands and quantified the difference in avian composition between vineyard and riparian habitats and the boundary edge between the two habitats. We further tested whether the presence of nest boxes in vineyards and adjacent riparian areas altered the composition of avian species, compared to control areas without nest boxes. Finally, to characterize how vineyard expansion may be influencing avian conservation, we applied non-metric multi-dimensional scaling techniques to identify which bird species contributed most to statistical differences in avian species composition between habitats.

METHODS

Study Area.—Four vineyard sites with adjacent wooded riparian habitat along California's north coast were chosen for this study (Table 1). Sites A, B, and C were located in Mendocino County, California, USA adjacent to the Russian River, certified organic, and managed identically by the same grower. The fourth vineyard (Site D) was located in Sonoma County, California, USA adjacent to the wooded Sonoma Creek and Hooker Creek. The site was not certified organic; however, the manager applied sustainable, best management practices for chemical use (limited spray use included Roundup and a strobularin fungicide). In 2008, all four sites used Stylet Oil and sulfur to control insect pests, and sites A, B, and C occasionally received natural pyrethrin and Biomite to control leafhopper and spider mite populations, respectively. The vineyard habitat contained cover crops planted between rows of wine grapes (*Vitis vinifera*). The canopy vegetation of the riparian habitat was comprised primarily of: California live oak (*Quercus agrifolia*), valley oak (*Quercus lobata*), California buckeye (*Aesculus californica*), Oregon white oak (*Quercus garryana*), Pacific madrone (*Arbutus menziesii*), and California laurel (*Umbellularia californica*). The understory was dominated by Pacific poison oak (*Toxicodendron diversilobum*) but comprised of a diversity of shrubs and grasses typical of a Mediterranean climate.

Nest Box Treatment.—Each vineyard was divided in half and each half was randomly assigned as a control or avian enhancement (nest box) treatment. A buffer of ≥250 m was left between the nest box treatment and control areas based on neighbor distances of bluebird nests (Dickinson and Leonard 1996). Medium-sized "bluebird" nest boxes were constructed from redwood following recommendations of the North American Bluebird Society (2008; 13.9 cm by 10.2 cm by at least 23.8 cm tall with a 3.8-cm diameter entrance hole). Because avian species occupy vineyard boxes and defend territories from conspecific pairs, we erected boxes back-to-back in pairs within nest box vineyard treatments to maximize available nesting sites. Between November 2007 and January 2008, we placed 3–6 pairs of boxes on 3.1-m T-posts along grapevine trellises in treatment areas, spaced 85 m apart on the basis of nearest-neighbor distances measured by Dickinson and Leonard (1996).

Heaton et al. (2008) documented which avian species are likely to occupy nest boxes in vineyard and wooded habitats in California. All cavity-nesting passerine species in semi-open vineyard habitat are medium-bodied birds (14–29 g) that occupy "bluebird" sized boxes. Within wooded habitats, inhabitants include medium-sized species, as well as smaller-bodied wrens and chickadees (9–12 g) that inhabit "wren" sized boxes with 28-mm diameter entrance holes (e.g., Bewick's Wren, *Thryomanes bewickii*). To accommodate these differences, nest boxes of two different dimensions were placed every 12.5 m in the riparian areas of the nest box treatment: (1) the medium-sized "bluebird" boxes and (2) smaller "wren" boxes. Smaller boxes were made of cedar and placed every 25 m, randomly alternating orientation between north, west, south, and east. Half of these were mounted on 1.5-m T-posts pounded into the ground. Nest boxes were positioned such

TABLE 1. Alphabetical code indicating study site characteristics and locations in California, USA.

Site	Size (ha)	Elevation (m)	Width of riparian zone (m)	Closest city*	Latitude and longitude
A	18.2	148	55–90	Hopland	38° 59′ N, 123° 06′ W
B	33.2	152	80–250	Hopland	38° 59′ N, 123° 06′ W
C	51.4	168	50–160	Ukiah	39° 04′ N, 123° 09′ W
D	48.6	52	40–140	Glen Ellen	38° 20′ N, 122° 29′ W

that boxes facing similar orientations were installed on poles and trees relatively equally. Medium-sized boxes were also placed every 25 m, and were positioned between smaller boxes, following the same orientation and placement methods as the smaller boxes (Fig. 1).

Avian Sampling.—During the avian breeding season from late April through mid-July 2008, avian communities were sampled monthly, with one site sampled each week. Transects of mist nets (four-tier, 36 mm mesh) began in the riparian habitat and ended in the vineyard. At each site, two transects located at least 100 m apart were placed in both the control and nest box treatments (Fig. 1). At each site, mist net captures from the two transects were pooled per treatment and do not represent independent samples. Mist nets in the nest box treatments were at least 350 m from control nets. Each transect consisted of two, 6-m long mist nets in the riparian habitat (within dense vegetation), one 12-m long mist net in the vineyard edge, beginning at vineyard trellises closest to riparian habitat and extending into the vineyard, and one 12-m long mist net in the vineyard, 100 m from the edge net. Nets were placed at ground level (0–2.8 m), opened just

FIG. 1. Vineyard map of Sonoma site (D) illustrating mist net locations (X) and nest box spacing in both vineyard (stars) and riparian (diamonds) habitats. No nest box control in lower left. Numbers are distances in meters.

before sunrise, checked and cleared every 25 mins, and closed 4–6 hrs later, depending on weather conditions. Captured birds were identified to species and fitted with uniquely numbered U.S. Geological Survey aluminum leg bands. We recorded the following data: band number, species, sex, mass, breeding status, age, net where captured, date, and time. Processed birds were released in close proximity to the net in which they were captured. To reflect changes in phenology, avian sampling was categorized into one of three 4-week long time periods during the breeding bird season, corresponding to: early (22 Apr–22 May; birds finding territories, building nests, some with eggs), middle (23 May–24 Jun; first broods are fledging, other nests with eggs), and late (21 Jun–23 Jul; second broods fledging, less singing). Each site was sampled for 2–3 consecutive days during each time period.

In nest box and control treatments, mist nets were sampled concurrently whenever possible, otherwise they were sampled on consecutive days. We did not sample birds on days with high winds, precipitation, or following chemical application in vineyards. Although sampling had to be adjusted for grower spray schedules, we attempted to equalize sampling effort across treatments and sites over the breeding season. Mist net-hours per 12 m of net were calculated according to Ralph et al. (1993) in order to quantify sampling effort. Mist nets were open for 1,066 net-hours combined at four vineyard sites with individual sites ranging from 248–295 net-hrs. More mist net-hours accrued in the middle of the season (mean = 19.6, SE = 1.6 versus early mean = 14.8, SE = 1.4 and late mean = 10.2, SE = 0.4), because of more favorable sampling conditions. Because net transects were opened and closed consecutively beginning in the riparian habitat and ending in the vineyard, hours of mist net sampling across microhabitats was equivalent. Sampling effort between control (530 net-hrs) and nest box treatments (536 net-hrs) was similar. Consequently, statistical comparisons did not necessitate standardization by net hours.

Statistical Analyses.—To examine whether avian species composition varied as a function of habitat (riparian, edge, vineyard), time (early, middle, or late in the breeding season), treatment (nest box or control), and site ($n = 4$), we used a PERMANOVA procedure, a distribution-free permutational ANOVA from the multivariate statistics software package PRIMER-E (Plymouth Routines in Multivariate Ecological Research) 6.1.3 described by Clarke (1993). We used the PERMANOVA to test for the main effects of habitat, time, treatment, and site, including all two-way interactions. Because we were only interested in those effects, we excluded higher order interactions from the analysis. The similarity matrix used in the PERMANOVA was based on presence-absence of all captured species, rather than abundance (Clarke 1993, Anderson 2001) and as such our sampling unit is presence or absence of bird species in mist net captures per habitat per day. Because data are binary and the approach is permutational, there is no assumption of normality. Such an approach uses zeros, instead of being overly sensitive to them, resulting in a robust statistical comparison of avian captures in mist nets. Pseudo-*F*s and permutational *P*-values are reported for main effects of the model. Subsequent pair-wise tests were used to evaluate differences in main effects and corresponding *t*-values and permutational *P*-values are reported in text. Terms that were found to be significant in the non-metric multi-dimensional scaling PERMANOVA technique were evaluated with the SIMPER procedure, which is also included in PRIMER-E. This procedure evaluates the contributions of individual species to the significant terms.

RESULTS

A total of 536 individual birds from 43 species were caught in mist nets during the 2008 breeding season (Table 2), and 34 individuals from 12 species were recaptured. In the riparian habitat, 32 different species were captured compared to the vineyard and edge habitats that each contained 23 species. PERMANOVA results indicated that habitat, site, time, and the interaction between site and habitat all contributed significantly to differences in species composition (Table 3). Because of the significant interaction between site and habitat, we examined this interaction prior to the separate effects of either factor. Comparisons among treatment combinations in the site by habitat interaction revealed that riparian and vineyard habitats had different species composition ($P < 0.03$) at each of the four sites. Edge and riparian habitats differed in species composition ($P < 0.01$) for all sites except the Sonoma site D ($P = 0.15$). Species composition at edge and vineyard habitats did not differ at any site ($P \geq 0.05$ for all tests).

TABLE 2. All avian individuals (excluding recaptures) caught in mist nets by site and sampling location where R = Riparian, E = Edge, and V = Vineyard. The Woodland column indicates whether birds were sampled (Y = Yes and N = No) in point counts in dense oak woodlands of Sonoma County from Merenlender et al. (2009). The Sites column refers to the four sampling locations from Table 1. An asterisk (*) indicates cavity-nesting species known to occupy nest boxes. Species of special concern or species on watch-lists are written in bold font. A number sign (#) denotes non-native species.

Common name	Scientific name	R	E	V	Total	Woodland	Sites
House Finch	*Haemorhous mexicanus*	2	46	65	113	Y	A, B, C, D
Chipping Sparrow	*Spizella passerina*	1	37	33	71	Y	A, B, C, D
Western Bluebird *	*Sialia mexicana*	3	16	29	48	N	A, B, C, D
American Goldfinch	*Spinus tristis*	7	18	22	47	N	A, B, C, D
Song Sparrow	*Melospiza melodia*	43	1	1	45	Y	A, B, C, D
Lesser Goldfinch	*Spinus psaltria*	1	20	7	28	Y	A, B, C, D
Black-headed Grosbeak	*Pheucticus melanocephalus*	16	8		24	Y	A, B, C
Bewick's Wren *	*Thryomanes bewickii*	12		2	14	Y	A, B, C
California Towhee	*Melozone crissalis*	10	2		12	Y	A, B, C, D
Oak Titmouse *	***Baeolophus inornatus***	**5**	**5**	**2**	**12**	**Y**	**A, B, C, D**
Black Phoebe	*Sayornis nigricans*	4	5	1	10	Y	A, B, C
European Starling #	*Sturnus vulgaris*		2	8	10	N	A, D
Red-winged Blackbird	*Agelaius phoeniceus*		5	5	10	Y	D
Yellow-breasted Chat	***Icteria virens***	**9**	**1**		**10**	**N**	**A, B, C**
Brown-headed Cowbird	*Molothrus ater*	5	1	1	7	Y	A, B
Spotted Towhee	*Pipilo maculatus*	6	1		7	Y	B, C, D
Tree Swallow *	*Tachycineta bicolor*	6		1	7	N	C, D
Nuttall's Woodpecker	***Picoides nuttallii***	**5**		**1**	**6**	**Y**	**A, B, C**
Dark-eyed Junco	*Junco hyemalis*	4	1		5	Y	C, D
Lazuli Bunting	*Passerina amoena*		2	2	4	Y	A, C
Violet-green Swallow *	*Tachycineta thalassina*		3	1	4	Y	A, B, D
Anna's Hummingbird	*Calypte anna*	1		2	3	Y	A, D
Bullock's Oriole	*Icterus bullockii*	3			3	Y	B
Downy Woodpecker	*Picoides pubescens*	3			3	Y	B, C
Pacific-slope Flycatcher	*Empidonax difficilis*	3			3	Y	B
Warbling Vireo	*Vireo gilvus*	3			3	Y	B, C
White-breasted Nuthatch *	*Sitta carolinensis*	2	1		3	Y	B, C, D
Yellow Warbler	***Setophaga petechia***	**3**			**3**	**N**	**A, C**
American Robin	*Turdus migratorius*	1		1	2	Y	A, C
Bushtit	*Psaltriparus minimus*	1		1	2	Y	A, C
Lark Sparrow	*Chondestes grammacus*			2	2	N	A, C
Lincoln's Sparrow	*Melospiza lincolnii*		1	1	2	N	C
Olive-sided Flycatcher	***Contopus cooperi***	**2**			**2**	**Y**	**A, C**
Swainson's Thrush	*Catharus ustulatus*	2			2	N	B
Ash-throated Flycatcher *	*Myiarchus cinerascens*	1			1	Y	B
Brown Creeper	*Certhia americana*	1			1	Y	C
House Sparrow *#	*Passer domesticus*			1	1	N	A
House Wren *	*Troglodytes aedon*		1		1	Y	C
Mourning Dove	*Zenaida macroura*		1		1	Y	A
Northern Flicker	*Colaptes auratus*	1			1	Y	C
Northern Rough-winged Swallow	*Stelgidopteryx serripennis*		1		1	N	A
Orange-crowned Warbler	*Oreothlypis celata*	1			1	Y	C
Western Tanager	*Piranga ludoviciana*			1	1	Y	D
	Total Species Number:	32	23	23	43		

With respect to the main effect of habitat (noting the interaction described above), there was a significant difference in species composition between vineyard and riparian ($P = 0.001$), and edge and riparian ($P = 0.001$) habitats, but not between edge and vineyard habitats ($P = 0.21$). With respect to the main effect of site (again noting the interaction described above) pair-wise differences in avian species composition between three of the sites were not significant; however, site A had a different composition of species than the three other sites ($P < 0.006$).

TABLE 3. Main effects and two-way interactions from PERMANOVA testing differences in the presence and absence of avian species across habitats (riparian, edge, and vineyard), time (early, middle, and late in the breeding season), treatment (nest box or control), and site (n = 4).

Source	df	MS	Pseudo-F	P (perm)
Habitat	2	630.5	15.32	0.001
Time	2	110.9	2.695	0.006
Treatment	1	53.96	1.311	0.292
Site	3	145.6	3.537	0.001
Site x Time	6	50.64	1.230	0.240
Site x Treatment	3	34.98	0.850	0.598
Site x Habitat	6	84.72	2.059	0.001
Time x Treatment	2	66.00	1.604	0.135
Time x Habitat	4	61.49	1.494	0.100
Treatment x Habitat	2	36.43	0.885	0.575
Residual	76	41.16		
Total	107			

House Finch (see Table 2 for all scientific names) was the most commonly captured species, occurring almost exclusively in the vineyard and edge. In those same habitats, Chipping Sparrows, Western Bluebirds, American Goldfinches, and Lesser Goldfinches were commonly captured at all four sites. In contrast, Song Sparrows, Black-headed Grosbeaks, Bewick's Wrens, Oak Titmice, and California Towhees were the most commonly captured species in the riparian habitat. Presence of Song Sparrows in the riparian area contributed to 9.5% of the difference between riparian and edge avian species composition, followed by species associated with the vineyard edge, including House Finches (8.6%), Chipping Sparrows (7.7%), American Goldfinches (7.4%), and Western Bluebirds (6.3%; Fig. 2a). Presence of House Finches and Chipping Sparrows in the vineyard contributed 14.3% and 11.6%, respectively, to the difference between riparian and vineyard species composition, followed by Song Sparrows in riparian habitat (9.1%; Fig. 2b).

Regarding the presence of nest boxes, no significant treatment effect was found (P = 0.29), indicating that the species found in nest box areas did not differ from areas without

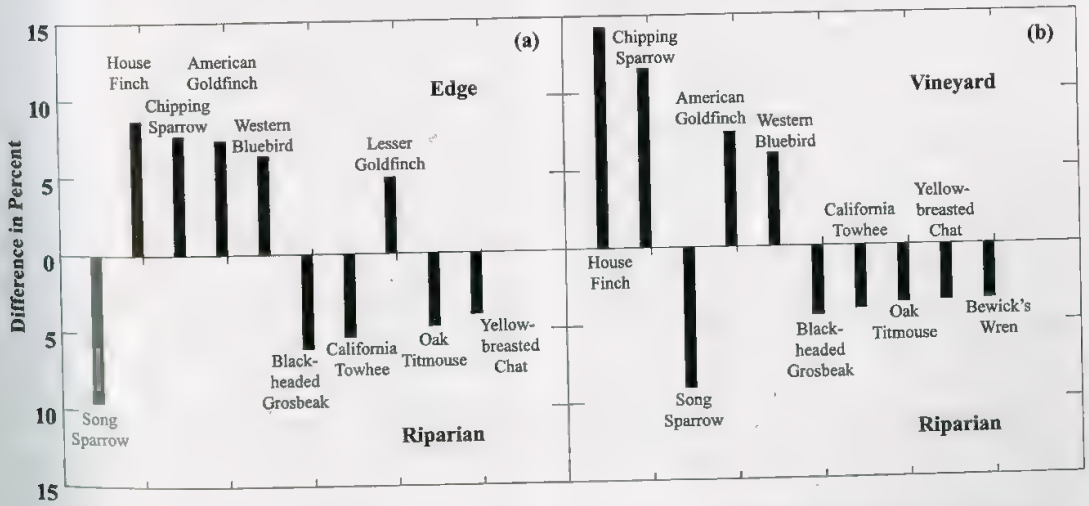

FIG. 2. Avian species (x-axis) responsible for contributing the highest percent difference (y-axis) distinguishing species composition in (a) riparian and vineyard edge habitats and (b) riparian and vineyard habitats. Bars arranged from highest contributor (left) and located below the midline to indicate species found principally in the riparian versus bars above the midline indicating more open habitats.

supplemented nesting sites (Table 3). All recaptured individuals were netted in the same treatments as they were found originally indicating the distance between control and nest box treatments was adequate. For the main effect of time only, the composition of avian species caught early in the breeding season differed from those caught in the middle of the breeding season ($P = 0.001$). However, differences in avian composition comparing late breeding season to early or middle were both not significant ($P \geq 0.2$ for all tests).

DISCUSSION

Vineyards contained several avian species that prefer semi-open habitat and were rarely captured in the riparian zone, including Western Bluebirds, Violet-green Swallows, Chipping Sparrows, Tree Swallows, American Goldfinches, and Lesser Goldfinches. Likewise, the assemblage of birds using the riparian habitat differed from those using the more open vineyard and transitional edge. This suggests the existence of a barrier at the riparian-vineyard edge boundary that many avian species do not cross. However, if species were found in the vineyard edge, they were also likely to venture farther into the vineyard because there was no difference in avian community composition between edge and vineyard associated birds.

Nest box establishment did not alter the avian species composition in vineyards or adjacent riparian areas. Cavity-nesting species associated with both semi-open habitat (e.g., Western Bluebirds and Violet-green Swallows) and riparian habitat (e.g., Oak Titmice and Bewick's Wrens) were found in both control areas and nest box treatments at most sites. While Jedlicka et al. (2011) observed increased abundances of Western Bluebirds in nest box treatments via point counts in subsequent years, our focus on community composition showed that the avian community did change between treatments. Sonoma and Mendocino wine grape growers interested in further supporting avian conservation should retain riparian vegetation (including snags) and maintain active nest box programs that increase vineyard bird abundance without drastically changing the vineyard avian community. Consequently, any avian-induced ecosystem services benefitting wine grape growers, such as insect pest control, are most likely associated with vineyard bird species such as the Western Bluebird (Jedlicka et al. 2011), and probably have little to do with the presence of riparian vegetation or woodland-affiliated avian species. Conversely, if growers have problems with pest bird species lowering grape yields, those species are associated with open agricultural areas and not affiliated with remnant riparian vegetation. Maintaining natural vegetation in agricultural landscapes does not harm grape production and offers habitat used by woodland-affiliated species declining in California.

The fact that woodland-affiliated bird species were captured almost exclusively in riparian habitat highlights the importance of maintaining natural areas, woodland patches, and habitat along streams in agricultural landscapes. Are bird species found in riparian habitats surrounded by vineyards similar to those associated with oak woodlands? In a recent publication on avian species composition in Sonoma County's oak woodlands, Merenlender et al. (2009) recorded bird species via point counts over a 5-year period. After narrowing Merenlender et al.'s list to those species likely to be captured in the 36-mm mesh mist nets used in our study (i.e., excluding birds > 80 g, such as birds of prey, and hummingbirds < 3 g), we sampled 32 of the 48 oak woodland associated species in riparian habitats of our study sites (Table 2). This indicates that riparian remnants may be important refugia for woodland avian species. In addition, we captured 12 species that were not sampled in Merenlender et al.'s point counts, most of which are associated with more open landscapes (Table 2). Because point count survey methods generally lead to greater detection of avian species (Whitman et al. 1997, Blake and Loiselle 2001, Derlindati and Caziani 2005), this comparison is likely conservative and may underestimate the conservation potential of wooded remnants in agricultural landscapes. In addition, most mist net studies only sample birds at ground level and some individuals may fly over the nets, avoiding capture. Differences in habitat structure can alter mean foraging heights of birds, along with their susceptibility to capture (Remsen and Good 1996). In this study, a structurally diverse, wooded riparian area was compared to a gridded monoculture of grapevines. Consequently, the greater vegetative height and complexity in the riparian area likely resulted in under sampling the riparian avian community, and the species list for this habitat is expected to be conservative when compared to grapevine trellises with no canopy.

Although we selected vineyard study sites to represent replicates of large vineyard blocks

adjacent to wooded riparian vegetation, site differences may reflect landscape effects or differences in riparian width. Riparian buffers at all our study sites were over 40 m wide, with some spanning up to 250 m in width (Table 1). This could have contributed to the relatively high species diversity we observed. A recent meta-analysis on faunal use of riparian areas indicates higher bird populations in riparian buffers than undisturbed riparian areas (Marczak et al. 2010), yet the authors found no effect of mean buffer width on species abundances. It is notable that site A, where avian composition was significantly different from the other three sites, was the smallest vineyard sampled and had the narrowest riparian width of up to 90 m compared to 140–250 m at the other sites.

We examined avian use of oak-vineyard landscapes during the breeding season; however, migratory species may also rely on corridors and agricultural habitats during stopovers and the non-breeding season. Avian populations in managed landscapes may also face difficulties such as low food availability during the non-breeding season (Dickinson and McGowan 2005) that need to be considered for informing avian conservation efforts. Early season surveys resulted in the capture of some migrants (e.g., Lincoln's Sparrows) and not strictly resident birds, perhaps contributing to the temporal differences found in the avian community over the course of the study. Alternatively, temporal differences observed may be a result of changes in foraging by avian species, in response to food availability and reproductive requirements.

We found the Oak Titmouse, a conservation priority of the American Bird Conservancy (ABC 2007) and Partners in Flight (PIF 2002), at all four sites in wooded riparian areas and, to a lesser extent, in vineyards. The Olive-sided Flycatcher, a species with declining populations listed as "near threatened" on the red list of the International Union for Conservation of Nature and Natural Resources (IUCN 2011), was captured in the riparian habitat at two sites (A and C). The Olive-sided Flycatcher is also on the watch-lists for ABC and PIF. More locally, the California Bird Species of Special Concern (Shuford and Gardali 2008) lists Olive-sided Flycatchers, Yellow Warblers, and Yellow-breasted Chats as threatened from habitat degradation. We primarily found Yellow-breasted Chats in the riparian habitat at three of the vineyard sites. In addition, Yellow Warblers were found solely in the riparian habitat of two vineyard sites. Finally, Nuttall's Woodpecker, a species with restricted distribution, low population size, and on the watch-list for PIF and ABC (PIF 2002, ABC 2007), was found primarily in the riparian habitat at three vineyard sites. Importantly, species presence in these patchy landscapes does not imply reproductive success. Reynolds et al. (2008) found that vineyard presence in the landscape did not impact nesting success or number of nests of oak woodland birds nesting in native habitat. Their finding suggests that vineyard landscapes may be able to support a productive and diverse bird community. Future research should analyze species-specific abundance, foraging, and reproductive success in riparian and vineyard habitats in order to determine whether riparian habitat in vineyard landscapes can provide suitable breeding habitat for declining bird populations. Here, we showed that avian diversity in remnant riparian areas of vineyard landscapes is relatively high and retains many species found in oak woodlands, along with riparian specialists such as Yellow Warblers and Yellow-breasted Chats. Maintaining natural areas, woodland patches, and riparian habitat enhances avian species diversity and is important for avian conservation in agricultural landscapes.

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DO AVIAN COMMUNITIES VARY WITH SEASON IN HIGHLY URBANIZED HONG KONG?

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ABSTRACT.—Urban habitat has become more and more important for birds because of rapid urban development and reduction of natural areas, and the responses of birds to season in urban habitats is important to research in urban avian ecology. We examined whether bird communities varied with season in terms of community attributes, composition of species and species groups, and nestedness in highly urbanized Hong Kong, which is positioned on one of the main migratory routes, and thus has great conservation value for birds. We studied 30 urban parks, and had 3,815 observations of 31 species in the breeding season (May–Aug 2010), compared to 3,972 observations of 53 species in the nonbreeding season (Nov 2010–Feb 2011). Eurasian Tree Sparrows (*Passer montanus*), Red-whiskered Bulbuls (*Pycnonotus jocosus*), and Japanese White-eyes (*Zosterops japonicus*) were the most abundant species in both seasons. Bird species richness and diversity in the nonbreeding season were significantly higher than in the breeding season. Migrants accounted for 5.0% of total abundance and 28.3% of richness in the nonbreeding season. Compared to the breeding communities, the avian communities included more insectivores (4.2%), insectivore-frugivores (4.8%) and herbivores (10.5%), but fewer granivores (8.4%) and species that feed on the ground (10.7%) appeared in the nonbreeding season. Moreover, multi-response permutation procedures analyses showed the composition of species and species groups differed significantly between the two seasons. Bird communities were highly nested in Hong Kong, but the degree of nestedness was close for the two seasons. We found there are obvious seasonal patterns in the bird community of Hong Kong, and an understanding of this can provide basic, essential information that park managers can employ to conserve a more diverse ecosystem in Hong Kong and even in other cities. *Received 17 June 2013. Accepted 26 October 2013.*

Key words: bird, guild, nestedness, park, Southeast Asia, urbanization.

Urbanization has rapidly increased, and it is estimated that, ~200,000 people on average will be added to the world's urban population each day between 2010–2015 (United Nations Human Settlements Programme 2012). With growing urban expansion, the effect of urbanization on bird community structure has become a hot topic in urban ecology (Chace and Walsh 2006). A large number of studies have been conducted on the effects of urbanization in urban greenspaces (Chace and Walsh 2006, Evans et al. 2011) and found urban development decreases species richness and leads to biotic homogenization. Various factors have been determined to affect urban birds, such as patch area (Fernández-Juricic and Jokimäki 2001, Suarez-Rubio and Thomlinson 2009, Oliver et al. 2011), vegetation structure (Fernández-Juricic 2004, Husté et al. 2006, Evans et al. 2009) and human disturbances (Marzluff et al. 2001, Fernández-Juricic 2002, Herrera-Montes and Aide 2011).

Seasonal changes and functional and structural responses by bird communities is an important research focus for community ecology, and many studies have been conducted in natural habitats and agroecosystems (Loiselle and Blake 1992, Kwok 1996, Kwok and Corlett 1999, Isacch et al. 2003, Meyer et al. 2010). Few studies have discussed the effects of season on birds in urban areas, and some conducted in Europe and North America have found that season affects species richness of urban bird communities and the nestedness pattern that occurs when species assemblages in relatively species-poor patches comprise successive subsets of the species present at richer sites (Patterson 1987, Suhonen and Jokimäki 1988, Wright and Reeves 1992, Jokimäki et al. 1996, Caula et al. 2008, Murgui 2010). Until now, there has been limited research on seasonal variation in birds in urbanized landscapes in Southeast Asia, especially in highly urbanized cities, such as Hong Kong.

Hong Kong features diverse habitat types (such as natural secondary forests, plantations, shrublands, grasslands, coastal wetlands, mangroves, inland ponds, densely constructed land and villages), and plays a pivotal role for migratory birds, because it is located on one of the main bird migration routes, i.e., the East Asia-Australian flyway (The Hong Kong Bird Watching Society

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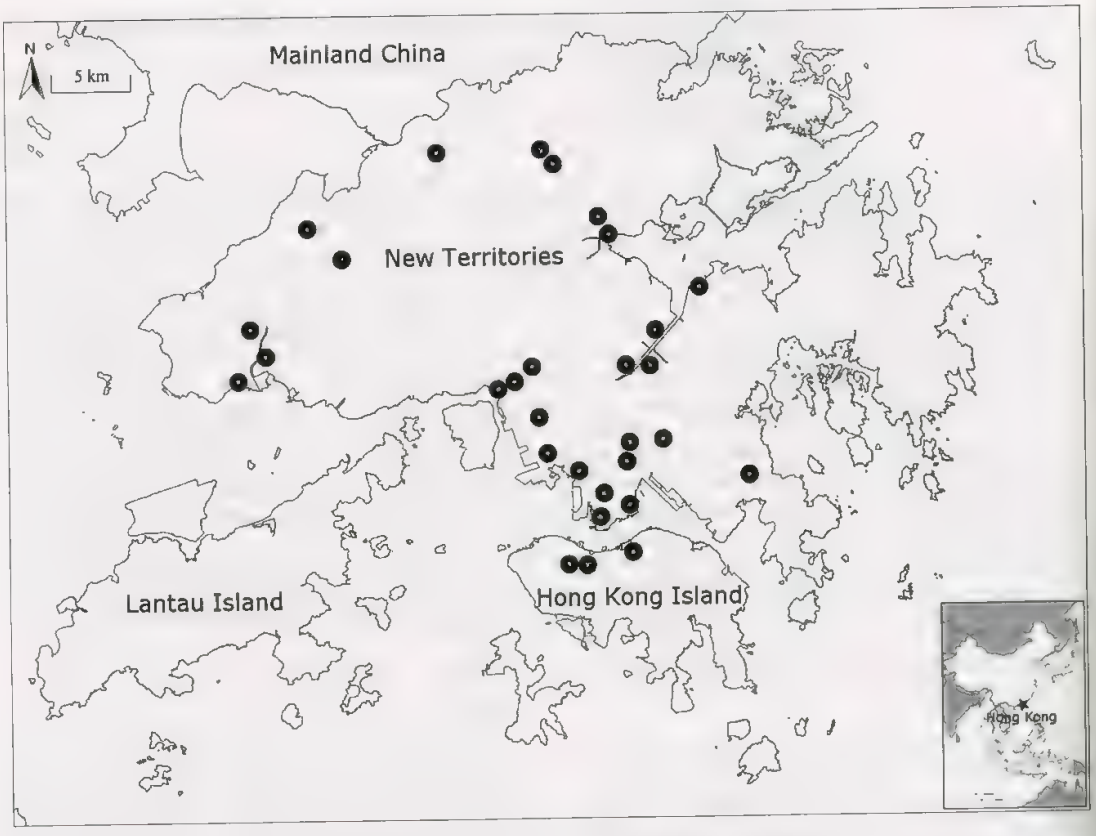

FIG. 1. Location of the 30 selected urban parks in Hong Kong.

Ltd. 2009). Hong Kong has many tropical bird species, but the climatic conditions are different from those in the tropics, because the rainfall and temperature are highly seasonal (Kwok 1996). Coupled with the high conservation values of its unique geographical location and significant seasonal climate, the seasonality of bird communities is of great interest in highly urbanized Hong Kong, where ~25% of land area is intensively exploited, and this land continues to be important as urbanization grows (Dudgeon and Corlett 1994).

Greenspaces in cities (e.g., urban parks, gardens, and greenbelts) have been demonstrated to be hotspots of avian diversity in urban landscapes (Adams 1994, Fernández-Juricic and Jokimäki 2001, Carbó-Ramírez and Zuria 2011), because they are important refuges and foraging sites for bird species, especially in areas with few greenspaces (Cicero 1989, Gering and Blair 1999). Actually, parks and gardens are the most important green pockets in urbanized Hong Kong (Lock 2000), and they are not only public amenity spaces but also biodiversity hotspots for urban birds (Lock 2000, Imai and Nakashizuka 2010). More knowledge about seasonal patterns of individual species or species groups would greatly contribute to the improved management of those important areas and stopover habitats for migrants.

For our study, we selected parks and gardens in urban Hong Kong as sampling sites and aimed to: (1) compare the avian community structure of urban parks in the breeding and nonbreeding seasons and (2) determine whether bird communities varied with season in terms of community attributes (species richness, diversity, and evenness), composition of species and species groups, and nestedness pattern. We predicted season would affect bird community structure in urban habitats in Hong Kong.

METHODS

Study Area.—Hong Kong (22° 09′–22° 37′ N, 113° 52′–114° 30′ E; Fig. 1) is a metropolis in Southeast Asia which is in the northernmost Asian tropics. Hong Kong has distinct seasonal characteristics

in temperature and rainfall, with a hot, wet summer (May–Aug; mean temperature = 27.8 °C, monthly average rainfall = 392 mm), and a cool, dry winter (Nov–Feb; mean temperature = 18.2 °C, monthly average rainfall = 35.9 mm) (1981–2010; Hong Kong Observatory 2013).

Hong Kong has a total land area of 1,104 km^2, of which ~6.2% are reclaimed from the sea. Hong Kong is hilly and highly urbanized, with more than 7.1 million people concentrating in less than 25% developed land area (population density: 6,507 individuals/km^2; Census and Statistics Department 2013). Most land (~ 70%) in Hong Kong is covered by various vegetation, but there is a shortage of greenspaces in urban areas, especially in developed areas (Lock 2000, Zhou and Chu 2012). There are more than 100 urban parks and gardens in Hong Kong, but almost all are <20 ha in area. Thirty parks (Fig. 1; park size: 1.0–19.1 ha) were selected as sampling sites based on the following criteria: (1) major central parks in Hong Kong; (2) scattered throughout Hong Kong (generally 2–3 parks for each administrative district) increases the representativeness of birds and parks; (3) sampling sites should have a gradient of land area and not have significant differences in park size; (4) sampling size should balance the workload because one survey would take place for all the sites; and (5) would need to be finished within a month. Most parks and gardens in Hong Kong are well managed by the Leisure and Cultural Services Department of the Hong Kong Government, and mean vegetation coverage of the 30 sampling sites reached to 62.5 ± 20.2% (mean ± SD; DZ and LMC, unpubl. data). However, those sites were surrounded by an average of 62.0 ± 17.7% constructed lands (such as roads and buildings) within 1,000-m radius landscape.

Bird Surveys.—Thirty parks were studied for their bird species composition once a month during the breeding (May–Aug) and nonbreeding (Nov–Feb) seasons in 2010–2011, using a fixed-radius (25 m) point count method (Hutto et al. 1986, Garaffa et al. 2009, Minor and Urban 2010, Carbó-Ramírez and Zuria 2011, Møller et al. 2012). Four counts per season were conducted for each park. The number of survey points for each park was determined based on its area, to make the sampling effort proportional to the area. Parks from 1.0–2.5 ha (n = 5) had 1 point, 2.6–5.0 ha (n = 5) 2 points, 5.1–7.5 ha (n = 5) 3 points, 7.6–12.5 ha (n = 8) 4 points, 12.6–16.0 ha (n = 5) 5 points, and parks >16.0 ha (n = 2) 6 points. Counts started as soon as the investigator reached the survey point, and the species and number of the birds seen or heard were recorded during a 10-min duration. However, birds flying over the survey circle or higher than the tree canopy were excluded. Generally surveys started at 0630 Hong Kong Time (HKT) and finished before 1030 on a dry day without strong winds (> 30 km/h).

Point counts could provide highly reliable estimates of relative population density, and it is a standardized and practical method to compare bird communities among different habitats and times (Bibby et al. 2000, Voříšek et al. 2008). To minimize the potential bias during bird surveys, first, we selected survey points using a random number table and gridded layouts. Survey points at a time were at least 100 m (> 200 m in large parks) apart. Second, survey points in the nonbreeding season were the same as those in the breeding season, to make the detectability of birds consistent between the two seasons. Third, we performed preliminary surveys to reduce the bias of distance estimation and enhance the investigator's familiarity with local birds. All surveys were conducted by the first author, which also made the species identification and bird counts highly consistent during the whole study period. Furthermore, we stopped bird surveys when temperature was high in summer, to reduce the negative impacts of high temperature on avian activities and detection rates. Finally, sites were investigated in reverse order during another visit to avoid time-of-the-day effects (Bibby et al. 2000, Rodewald and Yahner 2001, Møller et al. 2012).

Statistical Analyses.—First, species richness per season was examined by pooling all the survey data for each park. Second, Sørensen similarity index (Whittaker 1972) of bird communities of urban parks was determined for the breeding and nonbreeding seasons. Third, the diversity and evenness index for each park were calculated by averaging the four counts in the breeding/nonbreeding season. Each count of all the sampling points in a specific park were pooled, and Shannon diversity index and Pielou's evenness of the park were calculated for each count by EstimateS 8.0 (Colwell 2006). Standard deviation (SD) of Shannon diversity index, abundance-based coverage estimator (ACE) of species richness, and observation completeness (ratio of observed and expected number of species) were

used to assess whether our sampling efforts were sufficient for both seasons. We could regard our sampling effort as sufficient when estimated species richness did not strongly increase with the number of sampling sites or the SD of diversity index was very small (Colwell 2006).

We compared species richness, diversity, and evenness between the breeding and nonbreeding seasons by paired-sample *t*-tests. We also calculated relative abundance of each species, and compared the differences in species composition and relative abundance of the 10 most abundant species between the two seasons.

We categorized all the birds into different species groups, including residents (R), migrants (M), or introduced species (I) by their residency status; and frugivores (FR), granivores (G), insectivores (IN), insectivore-frugivores (IF), omnivores (O), or nectarivores (N) by food type. We also classified them into different species groups by their food substrate, including flower (F), air (A), ground (GD), shrub and low tree canopy (S), or upper tree canopy (T) (Kwok and Corlett 2000) (Appendix). We determined the number of species and the relative abundance for each species group, and assessed the differences in species composition of species groups and bird communities between the breeding and nonbreeding seasons using Multi-response Permutation Procedures (MRPP) (McCune et al. 2002). MRPP is a nonparametric statistical method that can be used to test the hypothesis that there are no differences in species composition between both seasons. Values of relative abundance were log-transformed prior to MRPP analyses to improve the linearity of relationships and reduce the range in values (Peck 2010). Sørensen (Bray-Curtis) distance measure and a natural group weighting method ($C_i = n_i/\sum n_i$, where n_i is the number of sampling sites in each group) were used to determine the differences in the species composition. Degree of separation between two groups was described by T, which is the test statistic of MRPP analyses. Greater negative value of T indicates more separation. Within-group homogeneity was compared to random expectation, and described by the chance-corrected within-group agreement (A). If all items within groups are identical, $A = 1$. If heterogeneity within groups equals expectation by chance, then $A = 0$ (McCune et al. 2002).

We conducted similarity percentage (SIMPER) analysis to identify the species that contribute most strongly to the dissimilarity between the two seasons (Clarke 1993). Original data matrix of species abundance for each park was used. A cut-off percentage of 80% was used during SIMPER analysis, so that species contributing to the dissimilarity in the two seasons were listed in descending order until 80% of the dissimilarity between seasons was detected. Average dissimilarity (*Dissim*) is the average contribution for each species to the overall dissimilarity. Larger values of the ratio of the average dissimilarity for each species to standard deviation for the Bray-Curtis species dissimilarity between two seasons (*Dissim/SD*), indicates those species that contribute much to the dissimilarity, but also have low variation in inter-comparisons of all samples in the two seasons. Contribution (*Contrib*) is the percentage of contribution for each species to the dissimilarity between the two seasons (Clarke and Warwick 2001).

Nestedness is a common pattern of species composition found in both natural fragmented habitats (Blake 1991, Seaman and Schulze 2010) and urban landscapes (Wright et al. 1997; Fernández-Juricic 2000, 2002; Chen et al. 2006; Platt and Lill 2006). To study the degree of nestedness of bird communities in urban parks and compare the differences between the two seasons, we conducted nestedness analysis using Nested Temperature Calculator (Atmar and Patterson 1995) which was a temperature method developed by Atmar and Patterson (1993). System temperature (T_{observed} and T_{random}) ranges from 0–100, and the degree of nestedness among parks decreases as the system temperatures increases.

MRPP and SIMPER analyses were performed by PC-ORD 5.32 for Windows (McCune and Mefford 1999) and Primer 5.2.8 for Windows (Clarke and Gorley 2001), respectively. Other statistical analyses were performed using SPSS 17.0 (SPSS Inc. 2008).

RESULTS

Sampling Effort and 10 Most Abundant Species.—There were a total of 7,787 observations of 56 species (24 families), including 3,815 (31 species) and 3,972 (53 species) observations in the breeding and nonbreeding season, respectively. The similarity index for breeding and nonbreeding bird communities was 66.7%. Cumulative species estimates (ACE mean ± SD) indicated our sampling effort was adequate for the avian communities in the breeding season in Hong

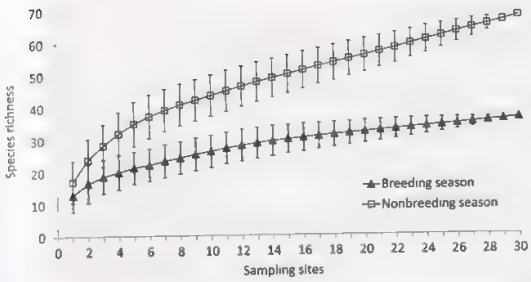

FIG. 2. Cumulative estimated species richness-sampling sites curve for urban parks in the breeding and nonbreeding seasons in 2010–2011 in Hong Kong. Estimated species richness is based on abundance-based coverage estimator (ACE), and error bars are SD.

Kong, with an observation completeness of 86%. However, sampling was slightly insufficient for the nonbreeding season (observation completeness = 78%), and estimated species richness marginally increased with additional sampling sites (Fig. 2). On the other hand, standard deviations of the cumulative Shannon diversity index was very low (< 0.01 for the maximal sample size) in both seasons, indicating that most species and individuals were recorded during the surveys, and only very few rare species might have been missed.

The 10 most abundant species in the breeding season accounted for 95.8% of total observations, compared to 89.9% in the nonbreeding season. Composition of the 10 most abundant species was very similar between the breeding and nonbreeding seasons (Table 1). Eurasian Tree Sparrows (*Passer montanus*), Red-whiskered Bulbuls (*Pycnonotus jocosus*), and Japanese White-eyes (*Zosterops japonicus*) were the three most abundant species in both seasons. Yellow-browed Warblers (*Phylloscopus inornatus*) were the only migratory species included in the 10 most abundant species in the nonbreeding season (Table 1).

Differences in Community Attributes and Composition of Species Groups.—Species richness and diversity were significantly higher in the nonbreeding season than those in the breeding season. However, species evenness did not differ significantly (Table 2).

In the breeding season, 26 residents were found, and the individuals counted accounted for a relative abundance of 99.6%. There were no migrants in the breeding season, while 15 species, accounted for 5% of total observations, were migrants in the nonbreeding season (Fig. 3A). For the food type, granivores, insectivore-frugivores, and omnivores were the three most abundant feeding guilds in both seasons (Fig. 3B). Relative abundance of granivores in the breeding season was 1.3 times as high as that of the nonbreeding season. On the contrary, species richness and relative abundance of insectivores and insectivore-frugivores were much higher in the nonbreeding season. Although the number of species that were omnivores was higher in the nonbreeding season, their relative abundance decreased slightly.

Regarding food substrate, urban parks in Hong Kong were mainly occupied by birds feeding on ground (GD), and shrub or tree canopy (S/T)

TABLE 1. Relative abundance of the 10 most abundant species in the breeding and nonbreeding seasons, and their residency status in Hong Kong in 2010–2011.

Species[a]	Residency status[b]	Breeding season (%)	Nonbreeding season (%)
Eurasian Tree Sparrow	R	28.9	15.7
Red-whiskered Bulbul	R	22.1	18.8
Japanese White-eye	R	12.8	18.4
Oriental Magpie-Robin	R	8.2	6.9
Light-vented Bulbul	R	6.5	9.9
Spotted Dove	R	5.8	10.4
Black-collared Starling	R	5.6	3.3
Common Tailorbird	R	2.2	—
Masked Laughingthrush	R	2.1	—
Feral Pigeon	R	1.7	1.8
Yellow-browed Warbler	M	—	2.8
Great Tit	R	—	2.0
Total abundance		95.8	89.9

[a] Refer to Appendix for scientific names.
[b] R = resident species; M = migratory species.

TABLE 2. Comparison of bird species richness, diversity, and evenness between breeding and nonbreeding seasons in Hong Kong. Values are means ± SD.

	Breeding (n = 120)	Nonbreeding (n = 120)	t-value/P[a]
Richness	6.92 ± 2.23	8.23 ± 3.03	−4.24/< 0.001
Diversity	1.57 ± 0.34	1.72 ± 0.39	−4.55/< 0.001
Evenness	0.84 ± 0.08	0.85 ± 0.09	−0.81/0.417

[a] Paired-sample t-tests between breeding and nonbreeding seasons.

substrates in both seasons (Fig. 3C). Compared to the breeding season, individuals feeding on the ground decreased ~12% in the nonbreeding season. However, relative abundance of birds feeding on various parts of plants (F/S/T) increased ~7% owing to the increased abundance of Japanese White-eye. Moreover, birds feeding on the upper tree canopy (T) increased greatly, both in the number and relative abundance of species. When the species classification of S/T, F/S/T, S, and T were combined, the results showed more species feeding on plants in the nonbreeding season (56.1%) than in the breeding season (45.6%).

Based on the MRPP analyses, the composition of introduced species ($T = 0.71$, $A = -0.04$, $P = 0.74$) did not differ significantly between the two seasons. However, resident birds ($T = -6.14$, $A = 0.06$, $P < 0.001$) were significantly different. For the feeding guilds, the composition of granivores ($T = -7.04$, $A = 0.06$, $P < 0.001$), insectivores ($T = -20.51$, $A = 0.21$, $P < 0.001$), insectivore-frugivores ($T = -2.24$, $A = 0.02$, $P = 0.04$), and omnivores ($T = -3.34$, $A = 0.03$, $P = 0.01$) significantly differed between seasons, but not for frugivores ($T = 0.39$, $A = -0.01$, $P = 0.57$).

Differences in Species Composition.—No birds were recognized as outliers. Bird species composition differed significantly between the breeding and nonbreeding seasons according to MRPP

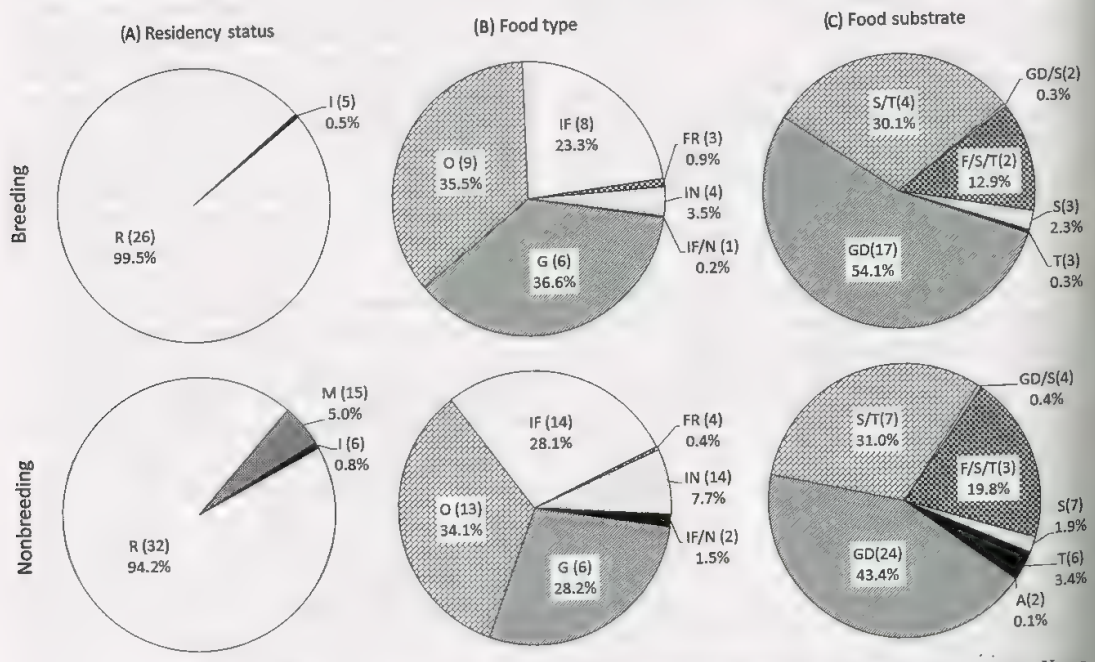

FIG. 3. Comparison of species groups between breeding and nonbreeding season in urban parks of Hong Kong. Relative abundance of each group was plotted, and the number of species of each group is shown in parenthesis following the abbreviated name. Species were categorized by residency status (A), food type (B) and substrate (C). For residency status: R = residents, M = migrants, I = introduced species. For food type: G = granivores, IN = insectivores, FR = frugivores, IF = insectivore-frugivores, N = nectarivores, O = omnivores. For food substrate: A = air, F = flower, GD = ground, S = shrub or low tree canopy, T = upper tree canopy.

TABLE 3. SIMPER analysis for the cumulative contribution of the first 10 bird species to the total average dissimilarity (82.2%) between the bird communities of breeding and nonbreeding seasons in 2010–2011 in Hong Kong.

Species[a]	Residency status[b]	Average abundance (ind/visit)		Dissim[c]	Dissim/SD[d]	Contrib (%)[e]
		Breeding	Nonbreeding			
Eurasian Tree Sparrow	R	275.5	156.3	6.2	2.8	25.0
Japanese White-eye	R	121.8	182.3	3.1	1.9	12.6
Spotted Dove	R	55.0	103.8	2.5	2.0	10.0
Red-whiskered Bulbul	R	212.5	186.5	2.2	1.5	8.8
Light-vented Bulbul	R	60.5	98.0	1.9	3.4	7.8
Yellow-browed Warbler	M	0.0	27.3	1.4	2.2	5.8
Black-collared Starling	R	52.8	32.5	1.1	1.9	4.3
Feral Pigeon	R	16.0	17.8	0.7	1.3	2.8
Oriental Magpie-Robin	R	78.0	68.5	0.6	1.1	2.6
Great Tit	R	7.8	20.0	0.6	2.0	2.5

[a] Refer to Appendix for their scientific names.
[b] Residency status of birds in Hong Kong; R = resident species, M = migratory species.
[c] Average contribution of a species to the total average dissimilarity.
[d] Ratio of the average dissimilarity of a species to standard deviation for the Bray-Curtis species dissimilarity.
[e] Percentage of contribution of a species to the total average dissimilarity.

analysis ($T = -8.80$, $A = 0.08$, $P < 0.001$). Additionally, SIMPER analysis indicated the average dissimilarity between the two seasons was 24.7%, and determined the 10 species that contributed to 80% dissimilarity between the two seasons (Table 3). The most abundant species in the breeding season was Eurasian Tree Sparrow, which accounted for 6.2% of average dissimilarity between the two seasons. Light-vented Bulbul (*P. sinensis*) and Yellow-browed Warbler were also reliable species which strongly discriminated bird communities of the two seasons (*Dissim/SD* > 2) (Table 3). It is worthwhile to note that all 10 species, with the exception of Yellow-browed Warbler, were resident birds in Hong Kong. These nine residents cumulatively contributed to 76.4% of the total average dissimilarity between the two seasons.

Nestedness Pattern of Breeding and Nonbreeding Bird Communities.—Bird communities in Hong Kong were highly nested in both breeding ($T_{observed} = 21.2$, $T_{random} = 62.6$, $SD = 4.4$, $P = 2.3 \times 10^{-21}$) and nonbreeding ($T_{observed} = 19.6$, $T_{random} = 62.0$, $SD = 3.8$, $P = 6.0 \times 10^{-28}$) seasons. Based on the observed T values, the degree of nestedness was close for the two seasons.

DISCUSSION

In our study of the effects of season on bird communities in a highly urbanized city, we found that bird communities varied with season in terms of species richness, diversity, and composition of species and species groups, but not for nestedness pattern.

Sampling Effort and Responses of 10 Most Abundant Species to Season.—According to the cumulative estimated species richness-sampling sites curve and small SD of cumulative estimated species diversity (< 0.01 for the maximal sample size), 30 sampling sites provided a reliable bird record for both seasons, especially for the breeding season (SD of ACE mean = 1.1; observation completeness = 86%). The estimated species richness increased with sampling sites in the nonbreeding season (SD of ACE mean = 2.1; observation completeness = 78%). Actually, 27 of 31 species recorded in the breeding season were also recorded in the nonbreeding season, which was further evidenced by the composition of the 10 most abundant species in the two seasons. Our results were consistent with those of the Hong Kong Breeding Bird Survey in 1993–1996, which determined the most widespread bird species in urban areas, including Eurasian Tree Sparrows, Spotted Doves (*Spilopelia chinensis*), Light-vented Bulbuls, Oriental Magpie-Robins (*Copsychus saularis*), Japanese White-eyes, Crested Mynas (*Acridotheres cristatellus*), and Red-whiskered Bulbuls (Carey et al. 2001). However, more migrants (such as Asian Brown Flycatchers *Muscicapa latirostris*, Dusky Warblers *P. fuscatus*, and Japanese Thrushes *Turdus cardis*) and rare forest-associated resident species (such as Hair-crested Drongos *Dicrurus hottentottus*, Orange Minivets *Pericrocotus flammeus* and

Scarlet-backed Flowerpeckers *Dicaeum cruentatum*) could be observed as the sampling sites increased, especially in the nonbreeding season. Therefore, more than 30 sampling sites would be necessary to study nonbreeding bird communities in urban landscapes in Hong Kong and even in other cities in East Asia and Southeast Asia (Zhou et al. 2012).

Responses of Richness, Diversity, and Species Groups' Composition to Season.—Kwok and Corlett (1999) found species richness and diversity in the nonbreeding season were significantly higher than that in the breeding season in a secondary forest of Hong Kong (i.e., Tai Po Kau Nature Reserve). We found the same pattern in an urbanized landscape in Hong Kong, which we attribute to the occurrence of 15 migratory birds in urban parks in the nonbreeding season. Resident species dominated the urban bird community in terms of species number and relative abundance in both seasons. This pattern has also been found in other East Asian cities such as Guangzhou (Li et al. 2008) and Shanghai (Yuan et al. 2011). The dominance by resident species was greatly enhanced in Hong Kong which indicated a higher degree of homogenization for bird communities (Zhou et al. 2012). However, obvious seasonal patterns for resident species were not found in six major urban parks in Hong Kong in another study (Lock 2000). Besides migrants, resident birds played an important role in the seasonal variations of bird communities.

Generally, food is likely to be more limiting for nonbreeding birds than those in the breeding season, especially in northern areas with climatic severity (Newton 1980, Jokimäki et al. 1996, Sherry et al. 2005). The availability of food resources in winter differs much from that in the breeding season in natural habitats, but this situation might be controversial when extending to urban landscapes, because of the supplementary foods provided by humans (Wilson 1994, Parsons et al. 2006, Evans et al. 2009). Lock (2000) found 82% of the total feeding observations for 28 species in six urban parks of Hong Kong were of supplementary foods (such as bread, rice, and seeds). Granivores and omnivores are major users of supplementary foods, and insectivores and insectivore-frugivores get fewer benefits from these anthropogenic provisions. We did not study the differences in food availability between the two seasons but speculate that supplementary foods may be less in the nonbreeding than in the breeding season because of fewer human activities in cold weather. This speculation was partially evidenced by the decreased abundance of granivores and bird species feeding on the ground in winter. On the contrary, relative abundance of insectivores and insectivore-frugivores feeding on plants (including flowers, shrubs, and tree canopy) were higher in the nonbreeding than the breeding season, possibly because of the various exotic plants cultivated in urban areas which provide food in winter.

Responses of Species Composition and Nestedness to Season.—Individual species composition varied significantly between the two seasons. Chan et al. (2008) detected significant seasonal differences in bird abundance of a secondary forest between wet and dry (equivalent to breeding and nonbreeding respectively) season in Hong Kong. Based on SIMPER analysis, nine resident species and one migrant contributed more than 80% of the average dissimilarity for the two seasons. In other words, the redistribution of resident species played a major role in the differences of bird abundance between seasons.

Murgui (2010) found the assemblages of resident, breeding bird species were significantly nested in the breeding season in Spain, but not in autumn and winter. The present study tested the hypothesis that nestedness pattern could be affected by seasonality. However, strong seasonality effects on the nestedness of urban avian communities were not detected in Hong Kong. This difference may be attributed to the severity of climatic conditions (i.e., the climate of Hong Kong was mild compared to Spain), and birds probably were less affected by the seasonal changes in habitat characteristics and food availability.

Conservation Implications.—Parks are generalized "islands" in an urban matrix that provide special habitats for birds. Bird communities in Hong Kong have obvious seasonal dynamics in terms of community attributes (species richness and diversity) and composition of species and species groups. Resident species dominated urban habitats, but urban habitats actually have become more and more important for migratory birds because of continued urbanization, not only in Hong Kong but also in other cities around the world.

Our study determined bird community structure and seasonal dynamics in urban parks of Hong Kong, and provides some basic information for biodiversity conservation. Moreover, we confirmed

that season does affect urban birds in Southeast Asia. We suggest areas with different vegetation structure and habitat types should be maintained in urban parks to increase heterogeneous habitats and food substrate, which would benefit migratory birds in winter. Moreover, how to conserve the migrants in urban fragmented habitats is a tough question that deserves further study.

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APPENDIX. Bird species observed in the breeding and nonbreeding seasons in the 30 urban parks of Hong Kong, and their classification into species groups.

Family	Species[a]	Residency status[b]	Food type[c]	Food substrate[d]
Columbidae	Spotted Dove (*Spilopelia chinensis*)	R	G	GD
	Feral Pigeon (*Columba livia*)	R	G	GD
	Emerald Dove (*Chalcophaps indica*)	R	G	GD
Cuculidae	Common Koel (*Eudynamys scolopacea*)	R	FR	S/T
	Greater Coucal (*Centropus sinensis*)	R	O	GD/S
Upupidae	Eurasian Hoopoe (*Upupa epops*)	M	IN	GD
Psittacidae	Rose-ringed Parakeet (*Psittacula krameri*)	I	FR	T
	Alexandrine Parakeet (*Psittacula eupatria*)	I	FR	T
	Blue-fronted Amazon (*Amazona aestiva*)	I	FR	T
Cacatuidae	Yellow-crested Cockatoo (*Cacatua sulphurea*)	I	FR	T
Motacillidae	Olive-backed Pipit (*Anthus hodgsoni*)	M	IN	GD
	White Wagtail (*Motacilla alba*)	R	IN	GD
Campephagidae	Grey-throated Minivet (*Pericrocotus solaris*)	R	IF	T
	Orange Minivet (*Pericrocotus flammeus*)	R	IF	T
Pycnonotidae	Red-whiskered Bulbul (*Pycnonotus jocosus*)	R	O	S/T
	Light-vented Bulbul (*Pycnonotus sinensis*)	R	O	S/T
	Chestnut Bulbul (*Hypsipetes castanonotus*)	R	O	S/T
	Black Bulbul (*Hypsipetes leucocephalus*)	M	O	S/T
Laniidae	Long-tailed Shrike (*Lanius schach*)	R	IN	GD
	Brown Shrike (*Lanius cristatus*)	M	IN	GD
Turdidae	Red-flanked Bluetail (*Tarsiger cyanurus*)	M	IF	GD/S
	Oriental Magpie-Robin (*Copsychus saularis*)	R	IF	GD
	Blue Whistling Thrush (*Myophonus caeruleus*)	R	IF	GD
	Japanese Thrush (*Turdus cardis*)	M	IF	GD
	Common Blackbird (*Turdus merula*)	M	IF	GD
	Grey-backed Thrush (*Turdus hortulorum*)	M	IF	GD
Sylviidae	Common Tailorbird (*Orthotomus sutorius*)	R	IN	S
	Dusky Warbler (*Phylloscopus fuscatus*)	M	IN	S
	Pallas's Leaf Warbler (*Phylloscopus proregulus*)	M	IN	T
	Yellow-browed Warbler (*Phylloscopus inornatus*)	M	IN	T
Cisticolidae	Yellow-bellied Prinia (*Prinia flaviventris*)	R	IN	S
Muscicapidae	Asian Brown Flycatcher (*Muscicapa latirostris*)	M	IN	A
Dicaeidae	Scarlet-backed Flowerpecker (*Dicaeum cruentatum*)	R	IF/N	F/S/T
Timaliidae	Rufous-capped Babbler (*Stachyris ruficeps*)	R	IN	S
	Masked Laughingthrush (*Garrulax perspicillatus*)	R	IF	GD
	Black-throated Laughingthrush (*Garrulax chinensis*)	R	IF	GD
	Hwamei (*Garrulax canorus*)	R	IF	GD
	Silver-eared Mesia (*Leiothrix argentauris*)	R	IF	S
Paridae	Great Tit (*Parus major*)	R	IN	S/T
Nectariniidae	Fork-tailed Sunbird (*Aethopyga christinae*)	R	IF/N	F/S/T

APPENDIX. Continued.

Family	Species[a]	Residency status[b]	Food type[c]	Food substrate[d]
Zosteropidae	Japanese White-eye (*Zosterops japonicus*)	R	IF	F/S/T
Fringillidae	Yellow-fronted Canary (*Serinus mozambicus*)	I	IF	GD
	Yellow-billed Grosbeak (*Eophona migratoria*)	M	IF	S/T
Corvidae	Asian Azure-winged Magpie (*Cyanopica cyana*)	I	O	GD
	Red-billed Blue Magpie (*Urocissa erythrorhyncha*)	R	O	GD
	Common Magpie (*Pica pica*)	R	O	GD
	House Crow (*Corvus splendens*)	I	O	GD
Sturnidae	Crested Myna (*Acridotheres cristatellus*)	I	O	GD
	Common Myna (*Acridotheres tristis*)	R	O	GD
	Chestnut-tailed Starling (*Sturnus malabaricus*)	M	O	S
	Black-collared Starling (*Sturnus nigricollis*)	R	O	GD
	White-shouldered Starling (*Sturnus sinensis*)	M	O	S
Dicruridae	Hair-crested Drongo (*Dicrurus hottentottus*)	R	IN	A
Passeridae	Eurasian Tree Sparrow (*Passer montanus*)	R	G	GD
Estrildidae	White-rumped Munia (*Lonchura striata*)	R	G	GD/S
	Spotted Munia (*Lonchura punctulata*)	R	G	GD/S

[a] Common names and scientific names of bird species follow The Hong Kong Bird Watching Society Ltd. (2009).
[b] R = resident species, M = migrants, I = introduced species. Residency status follows The Hong Kong Bird Watching Society Ltd. (2009)
[c] G = granivores, IN = insectivores, FR = frugivores, IF = insectivore-frugivores, N = nectarivores, O = omnivores. Food type follows Wu et al. (1988) and Kwok and Corlett (1999).
[d] A = air, F = flower, GD = ground, S = shrub or low tree canopy, T = upper tree canopy. Food substrate follows Wu et al. (1988), Kwok and Corlett (2000), MacKinnon et al. (2000), and Viney et al. (2008).

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FIRST DESCRIPTION OF NEST, EGGS, INCUBATION BEHAVIOR, AND NESTLINGS OF TRILLING TAPACULO (*SCYTALOPUS PARVIROSTRIS*)

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ABSTRACT.—*Scytalopus*, the largest genus of tapaculos (Family: Rhinocryptidae) typically build mossy globular nests within bank or tree cavities. Only 23 of the 40 recognized species' nests have been described, and of these only one has incubation patterns described. We provide the first description of the nest architecture, eggs, incubation behavior, and nestlings of the Trilling Tapaculo (*Scytalopus parvirostris*). The globular nest was mostly built of dark rootlets, and was lined with fern scales, hyphae, and feathers placed within the cavity of a rotting tree 1.5 m off the ground. The nest contained two white eggs. Nest attentiveness averaged 91 ± 0.5% per day, with an average of 12.6 ± 0.3 trips per day. Incubation bouts on the nest averaged 54.6 ± 2.9 mins and foraging trips averaged 8.8 ± 0.7 mins. Combined daily nestling growth rates averaged 18 ± 2% weight, 9 ± 2% tarsus, and 16 ± 3% wing (n = 4 days). *Received 1 April 2013. Accepted 2 November 2013.*

Key words: eggs, incubation pattern, nest, nestlings, *Scytalopus parvirostris*.

Tapaculos (Rhinocryptidae) are small understory suboscines, found in South and Central America (Krabbe and Schulenberg 2003). Similarities in plumage among species and their cryptic behavior in dense understory have made species delimitation challenging; however, use of molecular techniques and vocalizations have recently helped identify and diagnose new species (Cuervo et al. 2005, Mauricio 2005, Raposo et al. 2006, Donegan and Avendano-C. 2008). Difficulties observing tapaculos has also limited documentation of their general natural history, especially their reproductive biology (Krabbe and Schulenberg 1997).

The genus *Scytalopus* is the most diverse within the Rhinocryptidae, containing around 40 species (Krabbe and Schulenberg 1997, 2003). In the last decade, many new nests from *Scytalopus* have been described; however, 17 of the currently recognized species lack nest descriptions, and egg descriptions have been published for only 15 species (De Santo et al. 2002, Krabbe and Schulenberg 2003, Young and Zuchowski 2003, Greeney and Gelis 2005, Greeney and Rombough 2005, Arcos-Torres and Solano-Ugalde 2007, Decker et al. 2007, Pulgarin-R 2007, Hosner and Huanca 2008, Greeney 2008). Only single species have data published on nestling growth (Greeney and Gelis 2005) or incubation behavior (Decker et al. 2007).

Nests of *Scytalopus* are generally globular and made of moss, grass, or roots, and placed among roots, tree cavities, or short burrows (Krabbe and Schulenberg 2003). Usually two white eggs are laid, although some species appear to lay three, which may vary within a species because of variable habitat conditions (De Santo et al. 2002, Krabbe and Schulenberg 2003, Greeney 2008). Here, we present the first description of the nest, eggs, incubation behavior, and nestlings of *Scytalopus parvirostris*.

METHODS

We conducted fieldwork during the dry season, from August–December 2009 at the Wayqecha Biological Field Station (13° 10′ 30.1″ S, 71° 35′ 14.6″ W) in Manú National Park, Peru. Nest searchers walked 1 ha plots in subtropical montane cloud forest near 3,000 m at the edge of Puna grasslands. The study site had an annual average temperature 11.14 ± 0.5 °C.

When we encountered nests, we took measurements with calipers to the nearest millimeter, photographs, GPS coordinates, and recorded elevation. If eggs were present, we measured length and width with calipers (to nearest 0.1 mm), weight (to nearest 0.05 g), took photographs, and text descriptions. Two thermistors attached to a Hobo data logger (U-12 HOBO, Onset Computer Corporation, Pocasset, MA, USA, www.onsetcomp.com)

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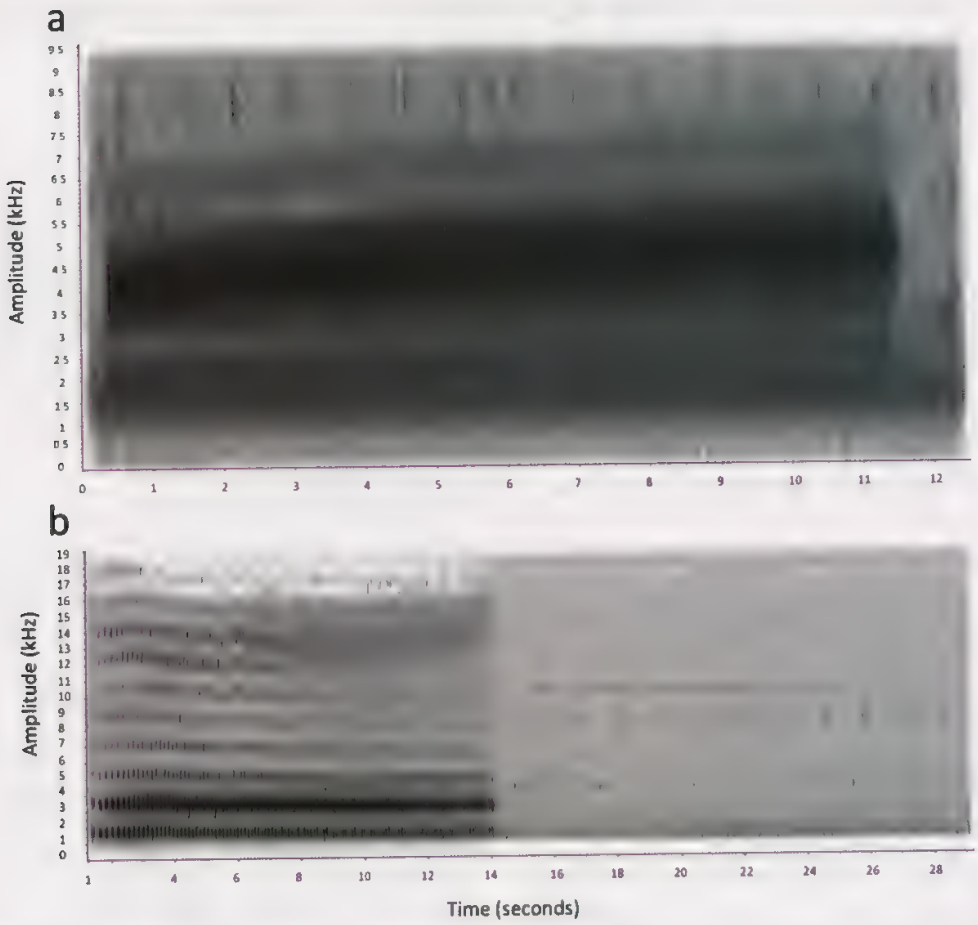

FIG. 1. Visual comparison of songs of *S. parvirostris* and *S. schulenbergi*. a) Song recorded by J. Jankowski in the vicinity of the nest. b) Song downloaded from www.xeno-canto.org/150484, recorded by D. Lane in Cotapata, La Paz, Bolivia.

recorded temperatures every minute until eggs hatched. One thermistor was placed inside the nest under the eggs and the other outside the nest (<15 cm). We used temperature fluctuation to monitor incubation behavior following Cooper and Mills (2005) protocol. Sensors were placed at the nest on 12 September and were removed 20 September, after nestlings had hatched. For the incubation behavior analysis, we only used complete 24 hour days (starting 13 Sep). We used changes in incubation behavior to estimate the hatching date because nestlings were first found in the nest a few days old.

Upon hatching, each chick was uniquely marked with permanent marker on their legs to differentiate between individuals, and daily descriptions and measurements (tarsus, wing, and mass) of individual nestlings were recorded. After the nest was depredated, it was collected, photographed, weighed, and its materials analyzed.

RESULTS

On 12 September 2009, G. Londoño and Michael Fuss were walking on a trail, and flushed an *S. parvirostris* (identified by visuals, video, and song), a few centimeters from its nest on the underside of a dead rotten tree (2,810 m, 13° 10′ 27.7″ S, 71° 35′ 40.9″ W). Adults were identified initially by species distribution, elevation, and habitat, and later corroborated by voice. Because *S. schulenbergi* can be found in the area and is hard to distinguish morphologically from *S. parvirostris*, we compared a song recorded from an individual in the vicinity of the nest (Fig. 1a) against an *S. schulenbergi*'s song (http://www.xeno-canto.org/150484; Fig. 1b). *S. schulenbergi*

FIG. 2. Nest (a), eggs (b), 4-day old nestlings (c), and 7-day old nestlings (d) of *Scytalopus parvirostris* from Manú National Park, Peru, 2009.

has higher amplitude, more frequent notes, and a longer duration.

Upon inspection, we found a globular nest tucked within a small natural cavity of the rotten tree, 1.5 m off the ground, in an excavated depression (Fig. 2a). The outer dimensions of the globe measured 119.4 mm high, 103.2 mm deep and 92.6 mm wide; the inner cup measured 50.0 × 57.0 mm, 25.1 mm deep (as measured from bottom of entrance), with a rim thickness of 41.2 mm. The nest was composed of two layers, the outer layer made of ~85% small rootlets, 10% dark green lichen, and 5% moss (cumulatively weighing 7.4 g); the inner cup was composed of 90% fern scales, 5% feathers, and 5% hyphae strings (cumulatively weighing 6.2 g). The nest contained two well-developed, unmarked, white eggs, the first measuring 19.3 × 22.5 mm and weighing 3.6 g, the second measuring 19.3 × 23.1 mm and weighing 4.05 g (Fig. 2b).

The nest was monitored during the last seven days of incubation and the adult(s) incubated continuously every night until the next morning, averaging 718 ± 4 (±SE) mins continuous incubation overnight. *Scyatolopus* averaged 12.6 ± 0.8 trips per day, averaging 8.8 ± 1.9 mins per foraging trip and 54.6 ± 2.9 mins per incubation bout. Incubation attentiveness (percent of time spent incubating, including nighttime) averaged 91.0% (min-max = 89–93%). Minutes spent off nest per day generally increased with egg develpment (r^2 = 0.51), but number of trips per day did not (r^2 = 0.001).

On 24 September, we revisited the nest site and found two nestlings (~4 days old; Fig. 2c), the smallest, henceforth "marked," and the larger

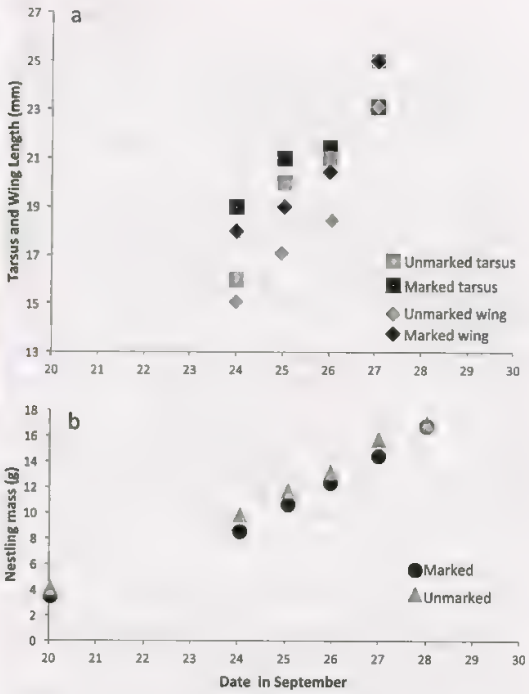

FIG. 3. Tarsus length, and wing length (a), and nestling mass (b) of *S. parvirostris*, plotted using dates in September 2009 in Manú National Park, Peru. Black color indicates marked nestling and gray indicates unmarked; squares indicate tarsus and diamonds indicate wing measurements. Egg weights (20 Sep; hatching date) and average adult female weight (29 Sep) are included for reference on graph of nestling mass. (a) Nestlings' tarsi and wing daily measurements in millimeters. (b) Nestlings' daily mass measurements in grams.

"unmarked" (Fig. 3). On 25 September, nestlings showed heavy down on wings, back, and head and the pins in the wings were just visible. On 26 September, the 6-day-old nestlings showed substantial development including open eyes, pin feathers on wings half emerged from the skin, and pins developing on the head, back, flanks, and tail. The nestlings' tarsi grew 9 ± 2% per day and wings grew 16 ± 3% per day (Fig. 3a), while weight gain averaged 18 ± 2% per day (Fig. 3b). On 28 September, we found the nest empty but completely intact. Nestlings would have been much too young to have fledged, and the nest was almost certainly depredated.

DISCUSSION

The new nesting information for *S. parvirostris* described in our study shows both similarities and differences from previous nesting descriptions of *Scytalopus*. Nest architecture and placement were

similar to other *Scytalopus*, which usually build mossy globular nests located inside cavities (Stiles 1979, Krabbe and Schulenberg 2003, Young and Zuchowski 2003, Greeney and Rombough 2005, Arcos-Torres and Solano-Ugalde 2007). Nests within the genus are built from a variety of materials including rootlets, moss, feathers, leaves, bamboo, or grass (Krabbe and Schulenberg 1997, 2003; Christian 2001; De Santo et al. 2002; Greeney et al. 2005); however, we report the first use of fern scales as nest material for this genus. The inner and outer nest dimensions of the nest were relatively similar to others previously described (Krabbe and Schulenberg 1997, 2003; Greeney and Gelis 2005, Greeney and Rombough 2005, Greeney et al. 2005, Arcos-Torres and Solano-Ugalde 2007). Most described nests of tapaculo were placed on the ground, unlike this nest of *S. parvirostris*, which was placed 1.5 m high in a tree cavity (Krabbe and Schulenberg 1997; although see De Santo et al. 2002, Decker et al. 2007).

Egg color and number are similar to those of other *Scytalopus* tapaculos; egg dimensions are also similar to those of other *Scytalopus* with comparable median female weights (Stiles 1979, De Santo et al. 2002, Krabbe and Schulenberg 2003, Greeney and Rombough 2005, Arcos-Torres and Solano-Ugalde 2007, Decker et al. 2007, Pulgarin-R 2007, Greeney 2008, Hosner and Huanca 2008). Incubation behavior in *Scytalopus* tapaculos has been documented in only one other *Scytalopus* species: Merida Tapaculo (*S. meridanus*) spent (±SE) 83.4 ± 14% of its time incubating eggs, and spent on average 33.24 mins on the nest and 6.34 mins off the nest (Decker et al. 2007). *S. parvirostris*'s nest attentiveness was higher than that of *S. meridanus* (averaging [±SE] 91 ± 0.5%), and bouts averaged longer on (54.6 ± 2.9 mins) versus off (8.8 ± 0.7 mins) the nest. Nest attentiveness of *S. parvirostris* is at the upper end of nest attentiveness reported for other Neotropical passerine species (min-max = 52.4–98.4%; Tielemen et al. 2004, Auer et al. 2007, Martin et al. 2007, Ocampo and Londoño 2011, Valdez and Londoño 2011).

Scytalopus micropterus and *Rhinocrypta lanceolata* (Mezquida 2001, Greeney and Gelis 2005) are the only other species with published data on nestling growth of tapaculos. Our growth rate data are preliminary, consisting of only 3 visits over 7 days. However, a preliminary comparison between *S. parvirostris* and *S. micropterus* (a larger species) shows weight gain averaged slower for *S. micropterus* (11.6 ± 1.2% and 18 ± 2% respectively), while tarsus growth rates were similar (9 ± 2% and 7.8 ± 0.6% respectively, Greeney and Gelis 2005).

Although we provide the first nesting biology information for *S. parvirostris*, much more information is needed to understand nesting strategies and requirements by this poorly known species and genus. Understanding basic nesting biology and natural history of a species is necessary for conservation initiatives.

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We thank M. Fuss for helping us to monitor and find nests. We also thank J. Oswald for providing valuable editing assistance. Financial support was provided by the Wilson Ornithological Society Louis Agassiz Fuertes Award, Journal of Field Ornithology, Pamela and Alexander F. Skutch Research Award, and the American Ornithologists' Union Alexander Wetmore Award. We want to thank the Asociación para la Conservación de la Cuenca Amazónica (ACCA) for their logistic support during our work in the Wayqecha biological station, and SERNAP for allowing us to work in Manú National Park.

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YOLK MASS VARIATION IN WHITE-RUMPED SWALLOWS (*TACHYCINETA LEUCORRHOA*)

MELINA BARRIONUEVO,[1,2] FLORENCIA BULIT,[1] AND VIVIANA MASSONI[1,3]

ABSTRACT.—Egg mass production is costly, but hatching from heavier eggs could be beneficial for the nestling's phenotype and fitness. Egg mass could be influenced by proximate causes, like food abundance, female condition, environmental conditions, and/or by ultimate causes, such as females depositing resources differentially within a clutch to increase the biological fitness of some eggs. Yolk mass, although poorly studied, is the source of nutrients for the embryo, so its mass should be more influential for the nestlings than total egg mass. We used a technique that allowed us to measure yolk size without destroying the eggs. We studied yolk mass in 212 eggs of White-rumped Swallows (*Tachycineta leucorrhoa*) and found that yolk mass was influenced by laying order, with last laid eggs having heavier yolks than first laid eggs, and the pattern was consistent with egg mass variation. Food abundance also affected yolk mass: when insect availability was high the yolks were heavier. We conclude that embryos in the last laid eggs have more resources from which to develop, and excluding food abundance, neither environmental conditions nor female's condition affected yolk mass. We encourage other researchers to study yolk mass given that multiple variables affected total egg mass. *Received 20 May 2013. Accepted 6 September 2013.*

Key words: egg mass, food abundance, proximate causes, *Tachycineta leucorrhoa*, yolk mass.

Egg production is expensive (Nager et al. 2000), because resources allocated to eggs are costly to the laying females (Perrins 1996) and thus, egg and clutch size are expected to be constrained (Lack 1947, Slagsvold and Lifjeld 1989, Zanette et al. 2006). Egg size is positively correlated with hatching success (Croxall et al. 1992, Perrins 1996), and many studies have determined the importance of egg size on the nestling stage (Williams 1994). In a recent review of egg size and offspring quality, Krist (2011) concluded that egg size was positively related to nearly all studied offspring traits across all stages of the life cycle. Therefore, egg size is considered an important life-history trait through which females could manipulate the phenotype of the offspring (Mousseau and Fox 1998, Gil 2003). Some studies suggest females could adaptively allocate nutrients differently to the eggs of the same clutch to produce within clutch egg-size differences (Howe 1976, Styrsky et al. 2002, Hargitai et al. 2005). Egg hormones are also responsible for within clutch egg variation as females can deposit them differentially and affect offspring phenotype (West-Eberhard 2003). It has been shown that laying order strongly influences androgen concentration in several bird species (Gil 2003), while in others, like Tree Swallows (*Tachycineta bicolor*), there is no apparent trend (Whittingham and Schwabl 2002). Other authors suggest egg size variation might be determined by proximate causes. The mechanisms invoked are related to female condition (Potti 1993, Smith et al. 1993, Ardia et al. 2006), laying date (Tsuboi and Ashizawa 2011), ambient temperature (Galbraith 1988), and the food abundance experienced by females during oogenesis (Ramsay and Houston 1997, Ardia et al. 2006, Whittingham et al. 2007).

Yolks are the principal source of nutrients for the developing embryo (Burley and Vadhera 1989, Deeming 2002), thus making it advisable to study not only total egg size but also egg content as a measure of parental investment (Astheimer and Grau 1990). Yolks are formed within the period of rapid yolk deposition (RYD), which occurs 3–10 days prior to egg laying (King 1973). In Zebra Finches (*Taeniopygia guttata*) this period lasts 3–4 days (Williams 2000), while in Tree Swallows yolks are formed 5–6 days prior to egg laying (Ardia et al. 2006). The albumin, containing 89% water and 12% proteins (Deeming 2002) is the major source of water and minerals for developing embryos; and the yolk, containing 48% water, 33% lipids, and 17% proteins is the primary source of energy and proteins (Burley and Vadhera 1989, Deeming

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2002). Egg yolks also contain androgenic hormones and steroids (Schwabl 1993), carotenoids (Bortolotti et al. 2003) and immunoglobulins, which provide the nestling's first immune response (Graczyk et al. 1994) and affect offspring survival and performance (Pilz et al. 2004).

Egg size is traditionally taken as a measure of maternal investment, but variations in egg mass do not necessarily imply variations in yolk mass, as a high percentage of the egg mass variation could result from differences in the amount of albumin and water content (Williams 1994). Yolk quality, indirectly measured as the yolk size, could have a determinant influence on a hatchling's weight or performance. Despite the physiological importance of this component, few studies have investigated the potential factors that determine the yolk size or mass, mainly because measuring it requires the destruction of the egg. However, digital candling allows measuring the yolk size in a large number of eggs without disturbing the developing embryos. Yolk mass has been studied using this tool in Tree Swallows in North America (Ardia et al. 2006), providing an opportunity to compare this trait with a South American congener and look for variations with latitude.

The objectives of this study were to analyze yolk mass variation within clutches of White-rumped Swallows (*Tachycineta leucorrhoa*), to determine potential factors related to this variation, and to establish if yolk mass can be directly inferred from egg mass. We predict that females in better condition, that breed early in the season, that experienced greater food abundance, and/or higher ambient temperatures during oogenesis, produce heavier yolks.

METHODS

White-rumped Swallows are insectivorous passerines that catch their prey in flight. The breeding season lasts 4 months; females lay 1 egg/day until they complete a median clutch of 5 eggs (range: 3–6 eggs), incubate the eggs for approximately 15 days, starting after the penultimate egg was laid, and the eggs hatch with a median asynchrony of 2 days (range: 1–4 days; Massoni et al. 2007). We conducted this study in a flat farming landscape in Chascomús, Buenos Aires Province, Argentina (35° 34′ S, 58° 01′ W) during the 2007 breeding season.

We checked nestboxes daily to determine clutch initiation date. On the laying day, we marked the eggs with sequential numbers in water-proof ink at the lesser pole to indicate the laying order, weighed the eggs to the nearest 0.005 g with an electronic balance and took a digital photograph of the eggs with a CANON Powershot A570 IS using both macro and no flash functions pointing into a dark box used to trans-illuminate the eggs. The black acrylic box measured 15 cm × 15 cm on its base and 20 cm of height, and was divided into two compartments: the upper one where eggs were laid on their side on a special support with the poles forming a line parallel to the base of the box, and the lower compartment where one white LED was connected to a battery (AA). The two parts of the box were separated by an opening through which the light of the LED passed to trans-illuminate the eggs. The design of the box was taken from D. R. Ardia (pers. comm.). When the camera was positioned in the opening in the box that was sized to match the diameter of its lens, the only source of light was that of the LED.

Using Image Pro-Plus 4.5 software we estimated yolk area. First, we transformed the yolk area from pixels to mm^2 by comparing the egg width measured in the field with a digital caliper (±0.01 mm) to the width measured on the screen (in pixels) using a subset of 15 eggs. Secondly, we transformed the yolk area (mm^2) into a mass estimation (g) using a subset of 18 collected eggs. After getting digital images of these 18 freshly laid eggs, we froze them (−20 °C), weighed the frozen yolks in a digital balance (±0.0001 g) and regressed the yolk mass on the yolk area (r^2 = 0.3; $P < 0.001$), obtaining the following equation to estimate yolk mass for the undisturbed, photographed eggs:

$$Yolk\ mass(g) = -0.12 + 0.0059 * yolk\ area\ (mm^2)$$

Females were trapped on the ninth day of the incubation period as described in Massoni et al. (2007). After sex confirmation (determined by the presence of an incubation patch), we measured head + bill length using a digital caliper (±0.01 mm) and weighed all captured individuals using a spring scale (±0.2 g). We estimated the females' body condition index as the residuals of the linear regression of their body mass on the head + bill length. To estimate food abundance, we daily collected samples of flying insects using two passive traps that intercepted the insects in flight, and used the total number of insects caught

by both traps on each day as an estimation of the amount of food available for the swallows (Barrionuevo et al. 2010). The traps consisted of 38 cm × 38 cm transparent acrylic squares resting on a plastic tray containing detergent and water, which served to retain the insects that collided with the trap. The traps caught many insects belonging to the same taxa and sizes found in the adult swallows' beaks when the birds were captured inside nest boxes during nestling feeding (Barrionuevo 2009). Traps were placed at the height of nest boxes because White-rumped Swallows spend significant amounts of time foraging at low altitude, capturing insects flying just over the pastures (VM, pers. obs.). The ambient temperature was recorded by the National Weather Center (Dolores Station, 89 km from our study site).

Statistical Analysis.—We analyzed yolk mass variations in 212 eggs, belonging to 47 nests with a linear mixed model with a Gaussian family distribution and an identity-link function. We only used first clutches and did not evaluate replacement second clutches because of the small sample size. We used nest identity as a random factor to account for the lack of independence of the eggs belonging to the same nest and clutch; the significance of random effects was tested with a likelihood ratio test. We considered as fixed predictors, the body condition of the female, clutch size, the laying date, and the laying order. As we were also interested in the potential effects of environmental conditions (temperature and food) on the yolk mass during egg formation, we added to the model as fixed variables the average of the daily mean temperature from the 5 days prior to the laying day of each egg, and the average of the daily total amount of insects collected 5 days prior to the laying day. We also included the following interactions: (1) laying order and insect availability, (2) female body condition and insect availability, (3) temperature and insect availability, and (4) laying date and female body condition. We employed a background selection procedure removing the terms one by one in decreasing order of complexity (interactions first) and *P*-value (Crawley 2007). After identifying the significant factors, we compared the model with and without the corresponding factor using likelihood ratio tests to estimate a unique *P*-value including all the levels of the factor. In the case of fixed variables, we conducted the same procedure to report concordant *P*-values. We used the "nlme" from the R software package, version 2.12.1 (R Development Core Team 2010) and report values as means ± SE, considering differences significant at $P < 0.05$.

RESULTS

Yolk mass was correlated positively and significantly with egg mass (Spearman rank order, $r^2 = 0.25$, $P < 0.001$, $n = 231$) and the yolk represented 30% of total egg mass ($n = 231$ eggs). Yolk mass ranged from 0.28–0.99 g (mean = 0.65 g ± 0.01 g), and egg mass ranged from 1.64–2.94 g (mean = 2.15 g ± 0.016 g). Insect abundance did not increase or decrease significantly across the broad time scale encompassing the laying period (mid-Sep to mid-Dec, $P = 0.95$), but we did detect important short-term oscillations (Fig. 1).

Random effects resulted in significant patterns ($\chi^2 = 56.87$, $P < 0.001$). Females that had access to greater food abundance during the egg formation period produced heavier yolks (L-ratio tests, $P < 0.001$), and laying order also affected yolk mass (L-ratio tests, $P < 0.001$). Within broods, we found no significant differences in yolk mass among the first three eggs (*t*-test; first vs. second and first vs. third: see Table 1; second vs. third: $t = -1.08$, $P = 0.28$) but their yolks were lighter than those from the last two eggs (contrast between the third and fourth yolk: $P < 0.002$), fourth and fifth yolks were also similar (*t*-test; fourth vs. fifth: $t = -0.11$, $P = 0.91$) (Fig. 2).

Neither of the other variables nor the interactions analyzed presented significant effects (L-ratio tests): female condition and laying date ($F = 0.67$, $P = 0.41$), female condition and insect availability ($F = 1.10$, $P = 0.29$), laying order and insect availability ($F = 8.95$, $P = 0.11$, Fig. 3), temperature and insect availability ($F = 0.48$, $P = 0.49$), clutch size ($F = 3.06$, $P = 0.38$), female body condition ($F = 2.22$, $P = 0.14$), temperature ($F = 0.089$, $P = 0.77$) and laying date ($F = 1.06$, $P = 0.30$).

DISCUSSION

The ratio between yolk and egg mass in White-rumped Swallows was slightly larger than that observed in Tree Swallows (0.30 vs. 0.26, respectively, Ardia et al. 2006); the yolk mass range was broader (0.28–0.99 g vs. 0.34–0.59 g, respectively) and the average mass heavier (0.65 g

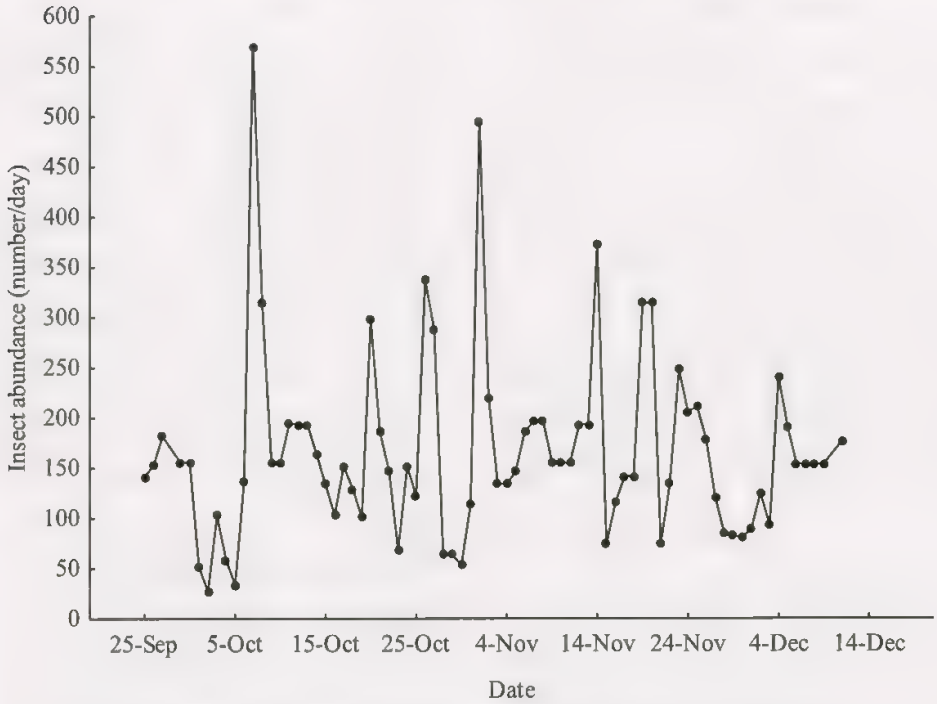

FIG. 1. Insect abundance (number of insects per day) during the laying season.

± 0.012 g vs. 0.47 g ± 0.001 g, respectively) in the South American species than in the northern one (this work, Ardia et al. 2006). Geographically, relatively larger eggs are generally found in the tropics and southern hemisphere relative to those in northern temperate zones (Martin et al. 2006), but the yolk to egg mass ratio comparison awaits further analysis across this genus.

The relationship between yolk mass and egg mass was statistically significant but weak. Moreover, in a previous study, we found significant variables affecting egg mass that are different from the variables affecting yolk mass (female body condition and ambient temperature did affect egg mass; Barrionuevo et al. 2010). These results indicate the relevance of considering egg and yolk mass to describe females' investment in egg production, as diverse ecological and/or individual factors may affect the deposition of different egg components.

TABLE 1. Results of the linear mixed model on yolk mass including insect availability, clutch size, laying order, laying date, temperature, female body condition, clutch size, and some double interactions. Only significant results are shown (n = 212 eggs, 47 first clutches).

	Estimate	t-value	P-value
Intercept	0.36	4.82	<0.001
Insect availability	0.0014	3.32	0.001
Laying order 2	−0.0027	−0.11	0.92
3	0.044	1.71	0.089
4	0.13	4.97	<0.001
5	0.13	4.57	<0.001

Insect availability during egg production in swallows is expected to be an important factor influencing egg mass (Nilsson and Svensson 1993) because they are "income" breeders, using the current food intake to produce the eggs (Winkler and Allen 1996, Nooker et al. 2005). We found that insect availability during the 5-day period before egg laying affected yolk mass, when food was scant yolks were lighter, irrespective of female body condition or laying order. This suggests that the resources acquired during yolk formation were directly invested into the yolk. Our results are in accordance with those of Ardia et al. (2006) who found a positive effect of insect availability in the days prior to the laying day in Tree Swallows' yolks, demonstrating its importance to the genus despite differences in latitude. Insect availability could affect egg size by constraining the females (Perrins 1970, Slagsvold

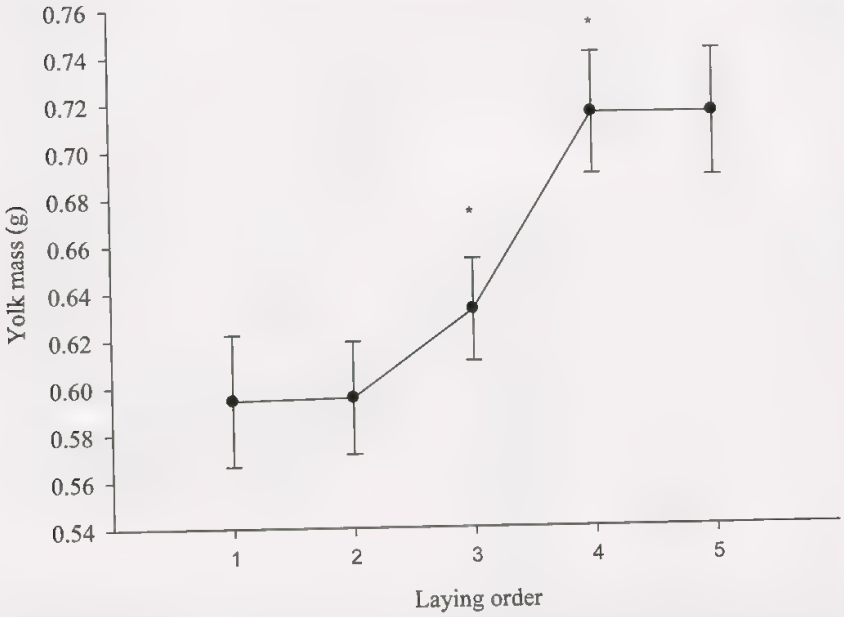

FIG. 2. Yolk mass according to laying order, error bars are ±SE and significant differences are shown with asterisks.

and Lifjeld 1989, Lifjeld et al. 2005) or because females use food availability as cues to establish their investment into eggs (Lack 1954, Arnold 1994, Hau et al. 2000).

We also found that yolk mass increased with laying order, contrary to Liljesthröm et al. (2012) who found no relation of yolk mass and laying order in the congeneric Chilean Swallow (*Tachycineta*

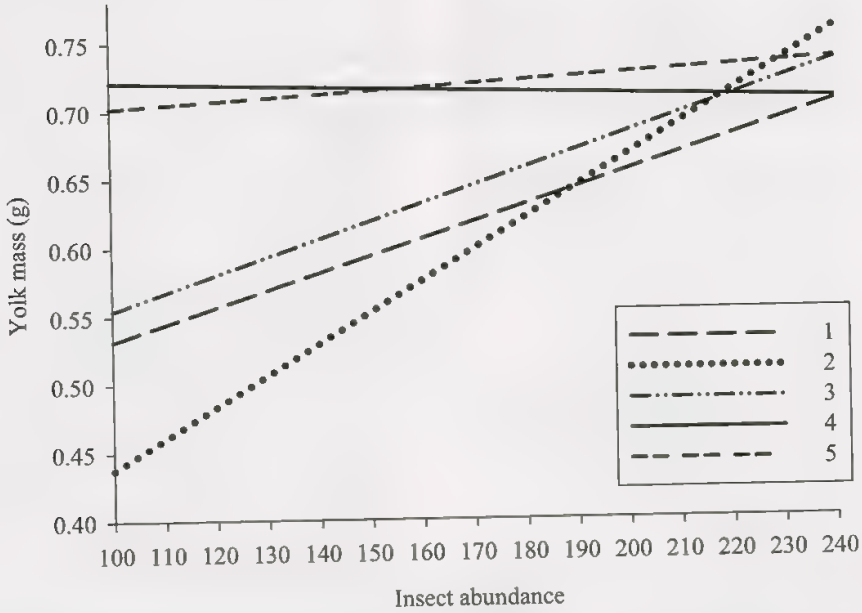

FIG. 3. Average insect abundance during the 5 days prior to the laying day vs. yolk mass for each egg of the clutches (1 = first laid egg, $r^2 = 0.042$, $F = 1.64$, $P = 0.20$; 2 = second laid egg, $r^2 = 0.044$, $F = 4.32$, $P = 0.84$; 3 = third laid egg, $r^2 = 0.055$, $F = 2.12$, $P = 0.15$; 4 = fourth laid egg, $r^2 = 0.0001$, $F = 0.006$, $P = 0.94$; and 5 = fifth laid egg, $r^2 = 0.001$, $F = 0.044$, $P = 0.84$).

leucopyga). In most avian orders, eggs hatch asynchronously because incubation begins before the clutch is complete (Stoleson and Beissinger 1995, Stenning 1996), resulting in a size hierarchy within the brood (Howe 1976, Aparicio 1999, Viñuela 2000). The last hatched eggs of White-rumped Swallows showed a median hatching asynchrony of 2 days compared to first hatched eggs (Massoni et al. 2007). Thus, if egg size is related with the size of the hatchlings, variations in egg size relative to the laying order may influence the degree of sibling competition. In Tree Swallows, Whittingham et al. (2007) found an effect of egg mass on nestling's quality, and Rosivall et al. (2005) found, in the Collared Flycatcher (*Ficedula albicollis*), that despite the last offspring having a lower body mass growth rate, the larger the last egg was, the smaller the growth rate lag of the offspring was. Howe (1976) suggested that an increase in egg size with laying order is an adaptation to counteract the effect of hatching asynchrony; the last eggs to hatch are bigger and compete better with already grown siblings. However, variation in size associated with laying order could be a consequence of proximate constraints, like daily changes in food abundance (Perrins 1970) or in temperatures (Ojanen et al. 1981, Järvinen and Ylimaunu 1986, Magrath 1992). None of these variables interacting with laying order were significant in our study. However, when plotting yolk mass and insect availability for each egg, a pattern was apparent, with differences between the first three eggs and the last two eggs. We believe these results did not reach statistical significance owing to sample size and further research is needed to ascertain their robustness.

The pattern observed in this study has been found in the Tree Swallow (Ardia et al. 2006), suggesting it may entail fitness benefits across the genus. As the yolk is the principal reservoir of nutrients (Deeming 2002) and where hormones and precursors of immune response are laid (Graczyk et al. 1994), the last chicks to hatch could have relatively more resources during initial development and would benefit from a better immune response and physiological quality.

Female condition was not related to yolk mass. Female condition is the integrated result of environmental conditions during migration and arrival at the breeding site, and during the pre-laying period; while yolk formation lasts only 5 to 6 days in the similarly sized Tree Swallow (Ardia et al. 2006). Female body condition was positively related to total egg mass (Barrionuevo et al. 2010); therefore total egg mass, which includes egg shell and albumin in addition to the yolk, is probably the product of energetically demanding processes lasting longer than the yolk formation process. Alternatively, the lack of an effect of female condition on yolk mass could be a consequence of delayed capture, since we measured female body condition 4 days after clutch completion. We believe that, though slightly imprecise because of the inclusion of days in which females incurred incubation costs, the index of their body condition still reflected variation among the females. As we found an effect of female body condition on egg mass on the same data set (Barrionuevo et al. 2010), we reject this alternative.

In a variety of species, ambient temperature has been shown to affect the thermoregulatory capacity of females (Ojanen 1983). This relationship between the ambient temperature and the energy expenditure assigned into thermoregulation could limit the energy females are able to invest into yolk or egg production. However, we did not find any relationship between yolk size and ambient temperature. During the 2007 breeding season, temperatures at Chascomús were not low enough to compromise the thermoregulatory ability of females, averaging 18 °C from September 2007 to January 2008. Finally, temperature could have an indirect effect on yolk mass through its influence on the amount or activity of flying insects, which are critical for insectivorous birds (Taylor 1963, Eeva et al. 2000). Nonetheless, the interaction between temperature and insect availability did not affect yolk mass in White-rumped Swallows.

We encourage using this non-destructive technique in studies of egg investment because the yolk is the major source of nutrients for the embryo and yolk quality could be more influential on hatchling condition than total egg size. We conclude that yolk mass was related to food abundance and varied with the laying order following a pattern compatible with the brood survival hypothesis, which proposes that females invest more in last-laid eggs to mitigate the disadvantage of these last-hatched chicks, when competing for food with the earlier-hatched chicks (Slagsvold et al. 1984, Budden and Beissinger 2005).

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RISKY EDGES: TEMPORAL VARIATION IN BROOD PARASITISM OF NORTHERN CARDINALS

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ABSTRACT.—Forest edges are often associated with a high risk of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*), but the extent to which this vulnerability changes across the breeding season is poorly understood. We evaluated temporal variability in the relationship between distance to habitat edges and risk of brood parasitism. From 2008–2010, we monitored parasitism of 347 nests of Northern Cardinals (*Cardinalis cardinalis*) at 19 forested sites within the urbanizing landscapes of central Ohio. For each nest, we measured distance to the nearest edge (e.g., road, residential area, mowed field, agriculture, and natural area) and recorded when clutches were initiated. We found that risk of parasitism associated with edges varied with time of season. Early in the breeding season, risk of parasitism declined with increasing distance from edges. However, late in the breeding season, nests farther from edges had higher rates of parasitism. These patterns suggest that early in the season, cowbirds search for forest nests along residential and agricultural edges, whereas later in the season, cowbirds search the interior. Our results show that managers should consider temporal factors in generalizing about the risk that edges pose to nests. *Received 5 June 2013. Accepted 7 October 2013.*

Key words: breeding season, brood parasitism, edge, temporal variation.

Fragmentation is widely known to promote brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) (Robinson et al. 1995, Donovan et al. 1997, Thompson et al. 2002) by increasing the amount of habitat edges where cowbirds are most abundant (Askins 1995, Chalfoun et al. 2002). The association between cowbirds and edges reflects the fact that cowbirds commonly forage in open areas and fields (Rothstein et al. 1980, Brittingham and Temple 1983). Consequently, nests closer to open edges are often at greater risk of parasitism than nests located in forest interiors (Gates and Gysel 1978, Brittingham and Temple 1983, Hoover et al. 2006, Brodhead et al. 2007).

Previous studies have documented strong spatial and temporal variation in the risk of parasitism. For example, parasitism rates have been reported to be both higher (Gates and Gysel 1978, Brittingham and Temple 1983, Hoover et al. 2006, Brodhead et al. 2007) and lower (Hahn and Hatfield 1995, Sharp and Kus 2006) near habitat edges. Likewise, parasitism rates are known to vary temporally (e.g., Burhans 1997, Rivers et al. 2010), which may result from seasonal changes in foraging and/or reproductive behavior of cowbirds (Laskey 1950, Scott 1963, Hahn and Hatfield 1995). Yet, no research has examined spatiotemporal interactions and specifically how the association between parasitism and edge might vary across the breeding season.

We hypothesized that temporal changes in cowbird behavior (Laskey 1950, Scott 1963, Hahn and Hatfield 1995) would affect the spatial patterning of parasitism such that the risk associated with edges would vary seasonally. We took the first step towards testing this by examining spatiotemporal variation in brood parasitism of a common songbird.

METHODS

We used Northern Cardinals (*Cardinalis cardinalis*) as a focal species to evaluate seasonal variation in the relationship between brood parasitism and distance to edge. Cardinals in our system have a long breeding season throughout which they are frequently parasitized by cowbirds (Shustack and Rodewald 2011, Rodewald et al. 2013). Although long-term data from our system indicate that brood parasitism does vary among species, sites, and years, parasitism rates of cardinals (35% from 2004–2011) were generally comparable to other common understory hosts, such as Acadian Flycatchers (*Empidonax virescens*, 40%) and Wood Thrushes (*Hylocichla mustelina*, 44%) (Rodewald et al. 2013).

We monitored nests of Northern Cardinals in 19 mature riparian forest patches (>250 m long and ~115–565 m wide) in central Ohio, USA from April through August, 2008–2010. Cardinals nest in the understory and midstory strata of forests encompassing a wide range of heights of

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0.5–20 m (mean height = 2.87 m ± 0.04 SE, n = 2962 nests from 2004–2011; ADR, unpubl. data). Cardinals re-nest after both failed and successful nest attempts, sometimes as often as seven times per season (Kearns and Rodewald 2013).

We located nests of cardinals by observing behaviors of territorial pairs breeding within 3–5 ha areas in each forest site. Nests were visited every 2–4 days to determine the nest status either by observing parental behavior or checking the contents of the nest. Not all nests could be definitively assessed for evidence of parasitism (cowbird eggs or nestlings) because of the high rates of nest predation before contents could be checked and/or the difficulty viewing contents of nests >7 m in height (~5% of nests; ADR, unpubl. data). Thus, we limited our analysis to nests that had been confidently checked and included measurements describing nest placement. After nests failed or fledged, we used range finders (>25 m) and measuring tapes (<25 m) to measure the distance from the nest to the nearest forest edge, which was bordered by roads, residential areas, mowed recreational fields, agriculture, and/or natural areas such as grasslands or early successional habitat.

To test the possible influence of distance to nearest edge and Julian date on cowbird parasitism rates, we conducted a logistic regression using a generalized linear mixed model PROC GLIMMIX; SAS Institute 2012). We modeled whether or not nests were parasitized with distance to nearest edge, Julian date, and their interaction as fixed effects, and site as a random effect. To test for significance, we used a Wald test, and then displayed the results using parameter estimates from the model. We also assessed the relationship between distance to edge and Julian date with a Pearson correlation coefficient and nest height and parasitism with a two-sample t-test (PROC CORR and PROC TTEST, respectively; SAS Institute 2012).

RESULTS

Cowbirds parasitized 40% of cardinal nests in our sample (n = 347). The risk of parasitism varied with Julian date (β_{julian} = 0.028 ± 0.006, $F_{1,329}$ = 18.79, P < 0.001), distance to edge ($\beta_{distancetoedge}$ = 0.031 ± 0.012, $F_{1,329}$ = 7.04, P = 0.009), and their interaction ($\beta_{julian*distancetoedge}$ = −0.0002 ± 0.00008, $F_{1,329}$ = 5.86, P = 0.016). Early in the breeding season, the risk of parasitism was lower in nests that were farther from edges; however, late in the breeding season, nests farther from edge habitat had a higher risk of parasitism (Fig. 1). Overall, nest placement did not vary with season, as we found no correlation between distance to edge and Julian date (r = 0.03, P = 0.56). Height of parasitized nests was not significantly different from that of unparasitized nests (mean height = 2.24 ± 0.07 SE vs. 2.02 ± 0.09 SE respectively, P = 0.066).

DISCUSSION

Previous studies showing that risk of parasitism was greatest near habitat edges did not consider temporal variation in risk (Gates and Gysel 1978, Brittingham and Temple 1983, Hoover et al. 2006, Brodhead et al. 2007). However, we found evidence that the risk associated with edges varied across the breeding season, such that edges were associated with brood parasitism only early in the season. Late-season nests were more likely to be parasitized farther from edges, though we recognize that our fragmented study system lacked any true interior habitat (>250 m from an edge).

One possible explanation for the pattern that cowbirds switch to hosts in the forest interior later in the breeding season is to track foraging opportunities. Cowbirds are less reproductively successful when visiting areas that provide few food resources (Rothstein et al. 1980) and local parasitism rates can be indirectly determined by cowbird food resources (Gustafson et al. 2002). Although cowbirds generally tend to forage and parasitize hosts in different areas, females may concentrate all activities into the same areas when food is abundant (Gates and Evans 1998). Furthermore, during their laying periods, cowbirds require more insects as food (Ankney and Scott 1980a) and will select habitat based on invertebrate density (Morris and Thompson 1998). In our study system, forest patches surrounded by a greater amount of urbanization have a higher abundance of arthropods (Bakermans and Rodewald 2006), and it is likely that invertebrate densities are higher in forest patches than the matrix itself (Jones and Leather 2012). Thus, cowbirds may be spending more time foraging in forests for arthropod prey as the breeding season progresses, resulting in more parasitism of nests farther from the edge. The effects of forest fragmentation and urbanization on arthropod abundance vary however (e.g., Bolger et al. 2000, Debinski and Holt 2000), so future research comparing arthropod biomass

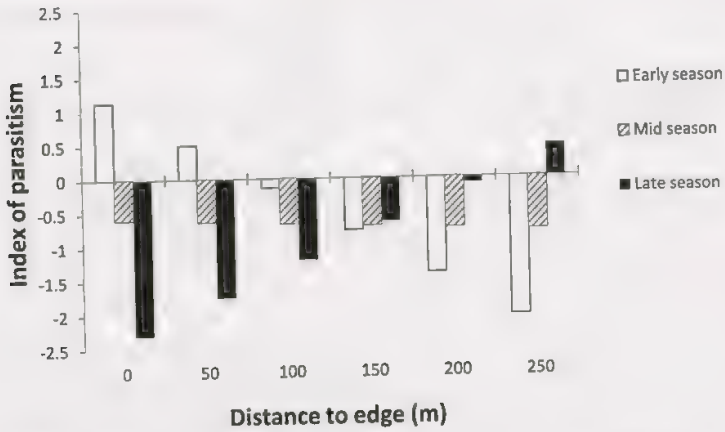

FIG. 1. Relationship of distance to edge and predicted risk of parasitism of nests of Northern Cardinals (*Cardinalis cardinalis*) by Brown-headed Cowbirds (*Molothrus ater*) as the breeding season progresses in riparian forests in Franklin and Delaware Counties, Ohio, USA. The breeding season was represented by early season (day 95), mid-season (day 158), and late season (day 220). We tested season as a continuous variable, but graphed it as a categorical variable. The index of parasitism was a function of the interaction between season and distance to edge.

between the forest patches and the matrix in our system will help verify our hypothesis.

An alternative explanation for our findings is that cowbirds are moving into the interior to search for alternative host species late in the breeding season when these alternative hosts become more active (e.g., Eckerle and Breitwisch 1997). For example, Rivers et al. (2010) found cowbirds will parasitize different host species at variable rates throughout the breeding season. In our system in particular, cardinals commence nesting earlier than many other host species (e.g., Acadian Flycatchers, Wood Thrushes, and Gray Catbirds [*Dumetella carolinensis*]; Rodewald et al. 2013). If cowbird reproduction is more limited by host nest availability than by resources (Ankney and Scott 1980b, Strausberger 1998), cowbirds may penetrate the forest interior to take advantage of more abundant hosts (Hahn and Hatfield 1995, Hosoi and Rothstein 2000) as the breeding season progresses. That said, of all the nests monitored in our system (37 species in total, with 12 species having >10 nests each), the mean distance to edge for species other than cardinals was 59 m, which is similar to the average of 49 m for cardinals. Thus, we lack strong support for the possibility that cowbirds shift away from edges to track late-arriving host species.

Previous research in our study system has suggested a strong seasonal signature on risk of nest predation (e.g., Rodewald et al. 2010, Shustack and Rodewald 2011), and we extend this to patterns of brood parasitism. Knowing that the burden of parasitism faced by a host species may change across the season is important in cases where biologists try to estimate the impact of cowbirds on host populations and, likewise, the relative value of edge versus interior habitats to birds (e.g., Askins 1995). However, further research is needed to see if the same pattern extends from cardinals to other host species.

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COURT CLEANING BEHAVIOR OF THE WHITE-BEARDED MANAKIN (*MANACUS MANACUS*) AND A TEST OF THE ANTI-PREDATION HYPOTHESIS

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ABSTRACT.—The cleaning of display courts is used by several forest lekking birds to possibly serve as an anti-predation strategy against terrestrial predators. Using a pit viper replica in the leaf litter 10–20 cm from the court (camouflaged predator) and in the central cleared area of the court (non-camouflaged predator) of the White-bearded Manakin *Manacus manacus* we tested experimentally the anti-predation hypothesis. We also described the phenology of court cleaning by lekking males, and tested the relationship between court cleaning and the frequencies of display bouts by males, visits to courts by females, and the amount of debris falling on courts. Results showed that court cleaning had a defensive role against terrestrial predators, optimizing the time of detection of potential terrestrial predators in the cleared courts. Court cleaning was positively correlated with court visits by females, which may be related to the improvement of a male's plumage conspicuousness by enhancing the plumage contrast against the cleared court, as already demonstrated for *M. vitellinus*. If this is the case, then court cleaning may serve a dual role, as an anti-predation strategy and to enhance sexual exhibition by lekking males. *Received 18 February 2013. Accepted 18 July 2013.*

Key words: Atlantic forest, lek, manakins, plumage conspicuousness.

Forest lekking birds such as manakins, cock-of-the-rocks, peacock pheasants, and birds of paradise may clean debris and pluck leaves from their courts on or near the forest floor (Gilliard 1959, Sick 1967, Johnsgard 1994, Endler and Théry 1996). A cleared court presumably signals ownership of a delimited display area by a resident male and the quality of the court owner for conspecifics (Uy and Endler 2004). Other possible functions of court cleaning include predation avoidance (Gilliard 1959) and optimization of light incidence on courts to improve male plumage contrast against background during displays (Uy and Endler 2004).

One hypothesis that has received little attention in the literature is that court-cleaning behavior serves as an anti-predation strategy to facilitate the detection of predators, such as lizards and snakes that lurk on or near the courts (Gilliard 1959). However, few instances of predation upon forest lekking birds (e.g., White-bearded Manakin *Manacus manacus* and Golden-headed Manakin *Ceratopipra erythrocephala*) were observed during long-lasting studies in the Neotropical region (Lill 1974a, b, 1976). Raptors were the main predators in leks of the Guianan Cock-of-the-rock *Rupicola rupicola* (Trail 1987). This conspicuous bird used spooks and alarm calls as anti-predation behaviors that apparently were efficient with raptors, but it has no known defensive mechanism against terrestrial predators, such as snakes (Trail 1987). Given existing evidence from other congeners that exhibit court-cleaning, it remains unclear if this behavior serves as an anti-predator function against terrestrial threats.

The court cleaning behavior was well described for the genus *Manacus* (Chapman 1935, Darnton 1958, Snow 1962, Sick 1967), but no studies have monitored the temporal variation or investigated the function of this as an anti-predation strategy. Individual males of *Manacus* have high survival, low rate of turn-over and extended periods of lek residency (maximum territory tenure 11.5 yrs; Lill 1974b). These characteristics suggest that either the predation pressure is low or that the anti-predatory strategy of lekking males is efficient. Using a snake replica in courts of the White-bearded Manakin, we tested experimentally the anti-predation hypothesis. To clarify the function of court cleaning behavior, we also described the phenology of court cleaning by male manakins and tested the relationship between court cleaning and the frequencies of display bouts by males, visits to courts by females, and the amount of debris falling on courts. We specifically addressed the following questions: (1) is court cleaning used to avoid terrestrial predators such as snakes, (2) how does the frequency of court cleaning vary throughout the year, and (3) is court cleaning

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correlated with the frequency of females' visits to courts? A positive correlation would be indicative of the role of court cleaning in sexual exhibition.

METHODS

Species.—Manacus manacus is a small (15–18 g) passerine that preferentially inhabits secondary forests of South America (Snow 1962). It is the most widespread manakin, with distribution extending from Colombia to northeastern Argentina (Snow 2004). Similar to most manakins, it is a dimorphic species; males have black on cap, back, wing, and tail, gray on rump, upper tail coverts, flanks and belly, and a white neck. Females are olive above, grayer and paler below (Snow 2004). Males display in classical leks where 2–70 individuals aggregate (Snow 1962, Olson and McDowell 1983). Each lekking male has an individual territory defended against conspecific intruders (Snow 1962, Lill 1974a). In each territory, a male has its own oval court of 0.15–0.9 m in diameter set on the ground and delimited by saplings (Darnton 1958, Snow 1962). During displays, an adult male makes loud snaps with his wings while leaping among the saplings that surround the court. Juveniles also practice display maneuvers in courts during periods when resident males are less active. Resident males frequently clean their courts during practice display bouts, and cleaning bouts become longer in duration before the peak period of breeding (Snow 1962). In Trinidad, Snow (1962) noted a well-defined post-breeding molting period for *M. manacus* during which displays of males are much reduced and molting males stay out of their courts for nearly 80 days.

Study Areas.—We conducted our study at six leks in the *restinga* ecosystem in lowland Atlantic forest, southeastern Brazil. Lek 0 with six resident males (24° 31′ S, 47° 12′ W), Lek 2 (four resident males; 24° 31′ S, 47° 11′ W), and Lek 3 (11 resident males; 24° 28′ S, 47° 7′ W) are located at Juréia Itatins Ecological Station (JIES) in Iguape municipality. Lek 4 with nine active resident males is located at Itanhaém municipality (24° 10′ S, 46° 55′ W), while Lek 5 (two resident males; 24° 15′ S, 46° 55′ W) and Lek 6 (six resident males; 24° 22′ S, 47° 2′ W) are located at Peruibe municipality. Distances between leks range from 9 to 49 km. Climate is subtropical and humid. Mean annual rainfall is 2,278 mm with the rainy season occurring October–April, and the dry season May–September. Mean annual temperature is 21.4 °C, with maximum and minimum temperatures averaging 25.8 °C and 19.0 °C, respectively (Tarifa 2004).

FIG. 1. A pit viper (*Bothrops jararaca*) replica (white arrow) on the cleared court area (A), and on leaf litter adjacent to the court area (B) of a lekking male of the White-bearded Manakin *Manacus manacus*.

Field Data.—To test if court cleaning behavior may act as an anti-predation strategy, we recorded the reaction of 21 males when presented to a resin replica of a pit viper (*Bothrops jararaca*), which is a potential terrestrial predator of small birds in the region (Marques and Sazima 2004, Marques et al. 2012). To the human eye, the replica is highly camouflaged on the leaf litter but can be detected easily in the bare soil of the court (Fig. 1). The snake replica was first placed on the leaf litter 10–20 cm from the court and then in the central cleared area of the court. If males reacted (with small escape flights and the emission of alarm "peerr" calls) to the snake replica, we assumed

that they detected the replica likely identifying it as a potential predator. Because previous studies indicate that resident males utter alarm "peerr" calls to any "unknown" object placed on the court (Snow 1962, Cestari and Pizo 2012, Coccon et al. 2012), before the experiment we placed a twisted twig with a shape similar to a coiled snake in the central cleared area of courts to verify if five different males distinguished it as a potential predator in five trials of 10 mins. All of them promptly uttered alarm calls, but in lower frequencies than during the experiment with the snake replica (t-test = 2.82; df = 4; P = 0.048). Furthermore, their close approaches to the twig (<10 cm; three of the males perched on it) with no escape flights allowed us to conclude that the males did not react to a snake-shaped object as a potential predator. Instead, the snake-shaped object was apparently only disturbing males' displays (Cestari and Pizo 2012, Coccon et al. 2012).

To begin each experimental trial, we profited from the brief periods of a male absence from its territory (usually for foraging) to silently put the replica adjacent to the court. Then, for 10 mins upon the return of the male to its court, we recorded the reaction or lack of reaction to the replica, the time to reaction (latency), and the frequency of alarm calls emitted. Twenty to fifty mins after setting the replica adjacent to the court, we put it in the court when males were again absent, and recorded the same data when males got back to their courts. Experimental trials took place during periods of peak activity in the lek (0610–0810 and 1240–1515, EST + 02). We performed the snake experiment with four males in Lek 0, two males in Lek 2, four males in Lek 3, six males in Lek 4, one male in Lek 5, and four males in Lek 6 from August–October 2011.

To monitor court cleaning phenology and test if court cleaning is related to sexual exhibition of *M. manacus*, we conducted observations of nine color-banded resident males from Leks 2, 3, and 4 (three individuals from each lek) from November 2009–October 2010. Each month, we observed the lek(s) from one study area (Itanhaém or JIES) for three sunny days. Thus, each study area was visited six times over 12 months. Observations followed the presence of resident males in leks, starting at dawn and finishing at afternoon or late afternoon. We divided the day in three equal periods lasting nearly 4.3 hrs each (0500–0920, 0920–1340, and 1340–1800) and observed one male at each period from concealed positions amidst the understory vegetation distant at least 5 m from the focal court. Males were observed in different periods during the days. From November 2009–October 2010, each male was observed 77.4 hrs. The following parameters were recorded for each male observed: (1) the frequency and duration of display bouts (displaying time), (2) the frequency of court cleaning bouts, and (3) the frequency of females' visits. A male display bout was defined as one uninterrupted sequence of leaps among court saplings. A court cleaning bout was recorded when a male picked up a fallen leaf, twig, or other debris from the ground and dropped it beyond the court edge or when a male perched on the ground and made short hovers to pull pieces of live leaves or rootlets that surrounded the court (Darnton 1958, Snow 1962). The presence of the observer apparently did not bother the lekking birds, as also reported by Darnton (1958).

Seven randomly distributed seed traps with areas similar to the area of courts (0.22 m^2) were used to sample fallen debris (leaves, twigs, and detritus) at Lek 3 from November 2009–October 2010. The material collected was dried and weighted in the lab, and mean dry biomass of fallen debris was correlated with the monthly mean frequency of court cleaning bouts. Similarity in vegetation physiognomies among lek areas allowed us to consider the biomass of fallen debris sampled at Lek 3 representative of Leks 2 and 4.

Statistical Analysis.—We used the G-test with Yates correction and a paired Student's t-test to test, respectively, for differences in the reaction of males (reacted or not) and the frequency of alarm calls emitted when the snake replica was on the leaf litter area adjacent to the court and in the central cleared area of the court.

Spearman correlations were used to test the relationships between the following averaged variables: daily frequency of court cleaning, duration of display bouts by males, daily frequency of females' visits, and biomass of fallen debris on courts. Because each study area was visited once every 2 months, data from both study areas were pooled resulting in bimonthly data for these analyses. Because court cleaning did not occur May–June 2010 when males were absent from leks (see results), for statistical analysis we added the mean biomass of debris during this period to the following July–August 2010 period. The software BioEstat 5.0 (Ayres et al. 2007) was

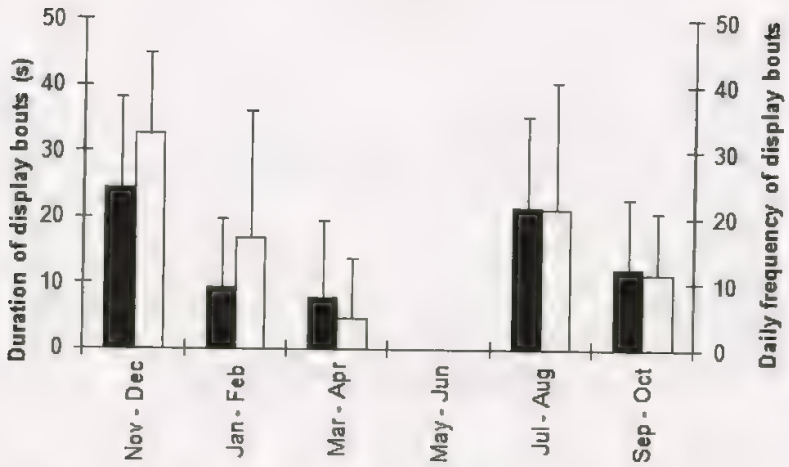

FIG. 2. Annual variation in the duration (black bars) and daily frequency of display bouts performed by nine lekking males of the White-bearded Manakin *Manacus manacus*. Vertical lines represent standard deviation.

used for all analysis. Significance was accepted at $P \leq 0.05$.

RESULTS

Seventeen out of 21 males detected the snake replica in the area with leaf litter adjacent to courts, whereas all the males promptly detected the replica in the central cleared area of courts, rendering no difference in detection probability ($G = 2.8$; df = 1; $P = 0.10$). However, there was a higher latency in the reaction of males for the emission of the first calls and short escape flights (24 ± 73.9 s, range 0–295 secs) when the snake replica was placed adjacent to courts compared to immediate reactions of males when the replica was in the court. The frequency of alarm calls by males when the replica was placed in the leaf litter (6.7 ± 6.5 calls/min, range 0–22.8) or in the court cleared area (5.7 ± 6.5 calls/min, range 0.2–21) did not differ (t-test = 0.8; df = 20; $P = 0.45$). A total of 10 lek-practicing juveniles and 10 neighboring adult males in six (28%) and nine (43%), respectively, of the experimental trials uttered alarm calls together with the experimental adult males. All of these juveniles and three neighboring males also entered in the territory of the experimental males to investigate the replica without being chased by the owner.

The daily frequency of court cleaning behavior was 1.80 ± 3.50 (range: 0–19, $n = 36$) with peaks between 0630–0700 and 1430–1500. Duration and frequency of displays abruptly increased in July–August and November–December, decreasing in March–April (Fig. 2). The frequency of court cleaning by males was positively correlated with duration of their display bouts ($r_s = 0.90$; $P = 0.020$) even when we removed the non-lekking period (May–June) from the analysis ($r_s = 0.87$; $P = 0.049$). Therefore, the probability of a male cleaning his court increased when the male displayed for longer periods, mainly during July–August and November–December (Fig. 3A). Similarly, the frequency of court cleaning and displaying time of males were positively correlated with the frequency of females' visits to courts ($r_s = 0.94$; $P = 0.005$ and $r_s = 0.82$; $P = 0.045$, respectively). These three parameters reached a peak in July–August and November–December (Fig. 3B, C). Additionally, there was a positive correlation between frequency of court cleaning and biomass of fallen debris ($r_s = 0.92$; $P = 0.007$) which peaked in July–August and November–December (Fig. 3D).

DISCUSSION

Lekking males of *M. manacus* detected the snake replica placed in their courts as well as in the leaf litter adjacent to courts where the replica was putatively better camouflaged. However, males did not react to the replica on the leaf litter as readily as they did when the replica was in the court, suggesting that the cleared area of the court contributed to make terrestrial predators such as snakes more conspicuous to males. In this sense, what matters to a successful predation upon *M. manacus* are the predator's position and camouflage amidst leaf litter together with its ability to develop a rapid strike to ensure a kill before

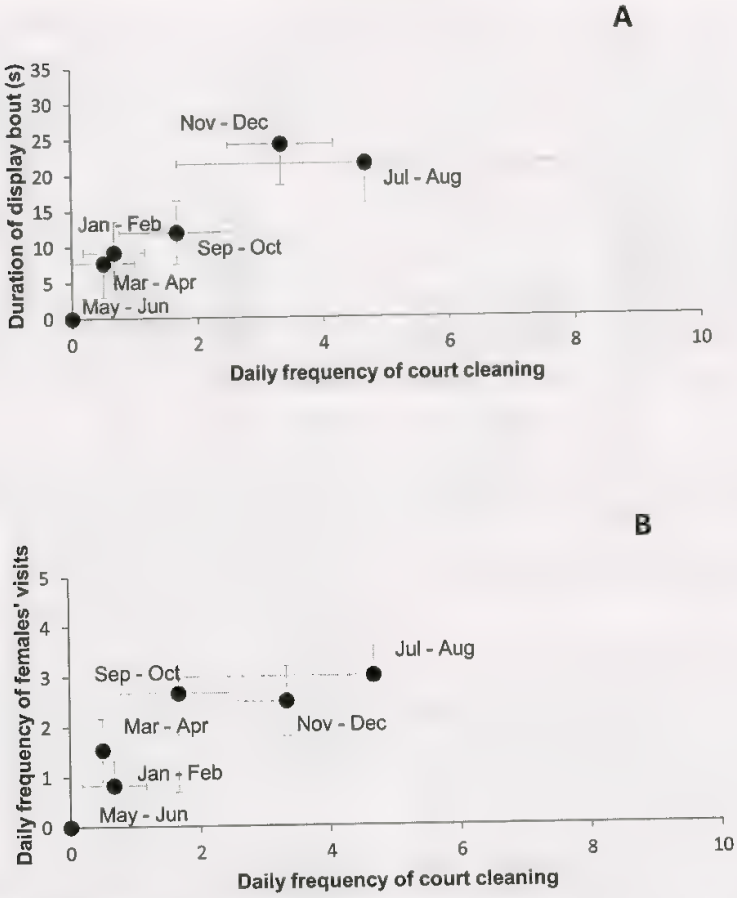

FIG. 3. Correlations between the mean frequency of court cleaning and mean duration of display bouts of males of the White-bearded Manakin *Manacus manacus* (A), mean frequency of court cleaning and mean frequency of females' visits to courts (B), mean duration of display bouts of males and mean frequency of females' visits to courts (C), and mean frequency of court cleaning and mean biomass of fallen debris (D). Vertical and horizontal lines represent standard errors. Nine resident males were observed at each 2-month period.

detection. Certain pit viper species can deliver a potent bite under a second (Marques and Sazima 2004, Marques et al. 2012), thus if well camouflaged in the leaf litter such a snake may potentially prey on *M. manacus*. The ability of lekking males to detect predators in the lek area was enhanced by neighboring adult and juvenile males that responded to alarm calls and entered the territories of experimental males to investigate the replica. This suggests that the combined attention of male manakins in leks can make them less vulnerable to predation, as also suggested for lekking Spotted Sandpiper *Actitis macularius* and *R. rupicola* (Oring and Lank 1982, Trail 1987).

The court cleaning behavior by resident males of *M. manacus* was positively correlated with the displaying time, frequency of females' visits to courts, and the biomass of fallen debris. These variables reached maximum values in the July–August and November–December periods. In the former period, males are returning from the molt (Snow 1962) and their courts are filled with debris. By this time, females initiate the recognition of potential mates by frequently visiting courts (Snow 1962, Lill 1974a). During this early-lekking period, males employed great efforts to clean their courts, while in the following months males did not clean the courts as often as in the early-lekking period (Jul–Aug) likely because of the small amount of litter to be cleaned resultant from their cleaning efforts in the previous months.

Apart from the detection of potential terrestrial predators, the court cleaning behavior of *M.*

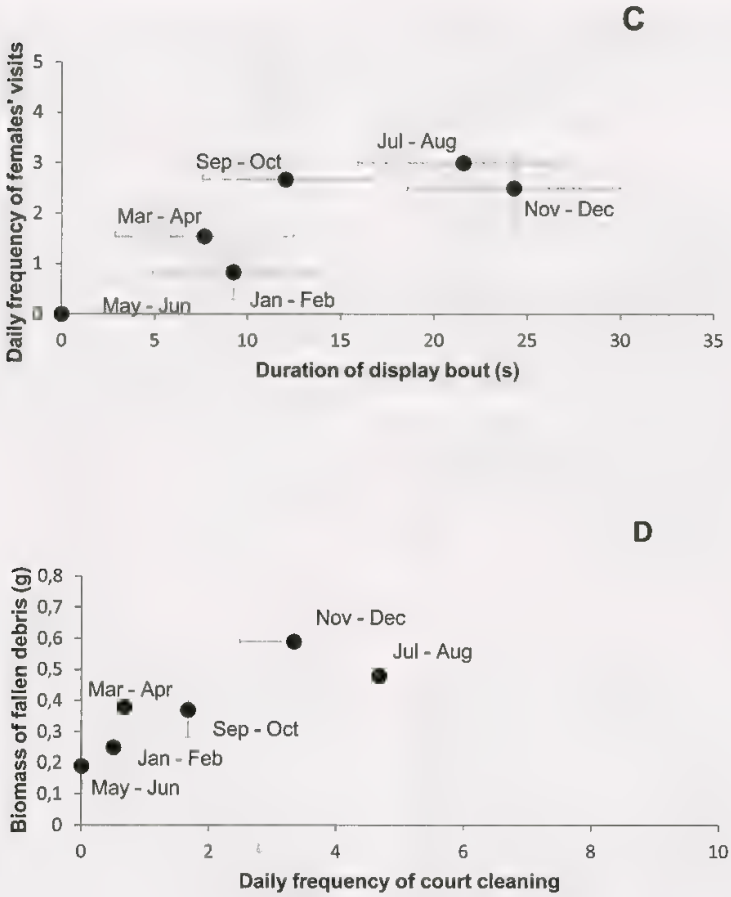

FIG. 3. Continued.

manacus may serve other purposes as well. For instance, the male plumage brightness and other lekking related traits (e.g., male size, aggressiveness, lek attendance, territory size and centrality, and plumage maintenance) are correlated with mating success in lekking birds (Snow 1962, Lill 1974a, Olson and McDowell 1983, Fiske et al. 1998, Cestari 2010). The court cleaning behavior may increase plumage conspicuousness by enhancing the plumage contrast against the cleared court as demonstrated for *M. vitellinus* (Uy and Endler 2004, Stein and Uy 2006). Therefore, the correlation we found between the frequencies of court cleaning and females' visits to courts may stem from this possibility. If this is the case, court-cleaning by lekking males maximizes predator detection in courts at the same time that it indirectly improves display performance, functioning in mate selection and ultimately contributing to reproductive success of lekking males. We encourage further investigations with *Manacus* manakins and other bird species with similar lek structure and behavior (e.g., *Rupicola* spp. and some *Pipra* spp.) to evaluate and disentangle the possible dual role of court cleaning, as an anti-predation strategy and to enhance sexual exhibition.

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FOOD RESOURCE EXPLOITATION STRATEGIES OF TWO REEDBED SPECIALIST PASSERINES: REED PARROTBILL AND ORIENTAL REED WARBLER

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ABSTRACT.—We studied the nestling diet of two reedbed specialist passerines, Reed Parrotbill (*Paradoxornis heudei*) and Oriental Reed Warbler (*Acrocephalus orientalis*) in a tidal reedbed in the Changjiang River Estuary, China. Reed Parrotbills delivered mainly Homoptera, Diptera, and Leptidoptera to their nestlings, and Oriental Reed Warblers delivered mainly Diptera, Hymenoptera, Araneida, and Lepidoptera to their nestlings. More than 98% of the diet of nestling Reed Parrotbills consisted of wingless items and >97% consisted of concealed items, indicating that Reed Parrotbills are limited in their ability to catch winged prey capable of strong flight and rather they retrieve prey from within reed shoots using their large and strong beaks. About 85% of the diet of nestling Oriental Reed Warblers consisted of winged items and >99% consisted of exposed items, indicating that Oriental Reed Warblers are limited in their ability to retrieve prey from within reed shoots and depend on their flight ability to catch prey capable of flight. Oriental Reed Warblers had significantly more taxonomic categories of prey in their diet, significantly wider diet niche, and significantly higher diversity in nestling diet than Reed Parrotbills. Our study demonstrates that although these two species breed sympatrically in reedbeds as reedbed specialist, Reed Parrotbills and Oriental Reed Warblers use different strategies in their exploitation of food resources. *Received 14 May 2013. Accepted 26 October 2013.*

Key words: *Acrocephalus orientalis*, habitat specialist, nestling diet, Oriental Reed Warbler, *Paradoxornis heudei*, reed bed, Reed Parrotbill, tidal marsh.

Food supply is often a limiting factor for birds during the breeding season, a time when breeding birds have to feed both themselves and their offspring (Martin 1987, Chamberlain et al. 2009). Birds depend on their beak to gather food and their flight apparatus to transport food items to their nestlings. Thus, both beak morphology and flight ability should play important roles in nestling diet composition (Carrascal et al. 1990, Marquiss and Rae 2002, Radford and Du Plessis 2003).

In reedbeds along the Changjiang River Estuary in China, the Reed Parrotbills (*Paradoxornis heudei*) and the Oriental Reed Warblers (*Acrocephalus orientalis*) breed sympatrically. Both species are insectivorous and are specialized for living and breeding in reedbeds (Catchpole 1974; Leisler et al. 1989; Lei and Lu 2006; Xiong et al. 2007; Xiong and Lu 2013a, 2013b). The Reed Parrotbill is a resident species restricted to reedbeds in East Asia (MacKinnon and Phillipps 2000, Lei and Lu 2006), while the Oriental Reed Warbler is a long-distance migrant and a summer visitor to reedbeds in East Asia (MacKinnon and Phillipps 2000).

Reed Parrotbills have shorter, wider, and deeper beaks than Oriental Reed Warblers (Fig. 1; also see Table 1 in Xiong and Lu 2013b), indicating the parrotbills have greater bite force than the reed warblers (Herrel et al. 2005). Thus, their strong beaks would help Reed Parrotbills in extracting prey from reed shoots (Xiong et al. 2007, 2010; Xiong and Lu 2013b); Oriental Reed Warblers are not able to utilize reed shoots because of their slender beaks, so they expand their foraging range more widely (Dyrcz and Flinks 2000, Xiong and Lu 2013). Reed Parrotbills and Oriental Reed Warblers use different strategies to live in reedbeds as habitat specialists.

There is a similar pattern in nest material and food resource exploitation for Oriental Reed Warblers and Reed Parrotbills (Xiong and Lu 2013b). Reed Parrotbills mainly use flightless insects found concealed within reed shoots (Xiong et al. 2007, 2010), and Oriental Reed Warblers collect their exposed, flighted insect prey on reedbeds and on plants close to reedbeds (Dyrcz and Flinks 2000). It may be the case that exploitation of exposed versus concealed items is related to the bill morphology of Reed Parrotbills and Oriental Reed Warblers, and the

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FIG. 1. Beaks of the Reed Parrotbill (top) and the Oriental Reed Warbler (bottom), note differences in depth and length between Reed Parrotbill and Oriental Reed Warbler (Photography by LHX).

exploitation of flightless (hereafter, concealed or wingless) versus flighted (hereafter, exposed or winged) items is related to the flight ability of Reed Parrotbills and Oriental Reed Warblers. If so, concealed items should dominate Reed Parrotbills' diet and exposed items should dominate Oriental Reed Warblers' diet, as concealed items are more easily captured by birds with weak flight abilities and exposed items are easy to be caught by birds with slender beaks.

In the present study, we studied the nestling diet of sympatrically breeding Reed Parrotbills and Oriental Reed Warblers in a tidal marsh at the Changjiang River estuary. We analyzed both the taxonomic composition and ecological traits (concealed versus exposed or flighted versus non-flighted) of nestling provisioning items. Our objectives were to examine the following predictions: (1) Reed Parrotbills deliver mainly wingless or concealed items to their nestlings and (2) Oriental Reed Warblers deliver mainly exposed or winged items to their nestlings, and to test whether Reed Parrotbills and Oriental Reed Warblers use different strategies in food resource exploitation.

METHODS

Study Area.—The study was conducted in the Chongxi Wetland Research Center (31° 42–44′ N, 121° 12–16′ E) at the west end of Chongming Island, Changjiang Estuary, China. The Center has a tidal marsh covered by monospecific stands of common reed (the reedbed). A belt of willows (*Salix* spp.) with a scattering of wild rice (*Zizania latifolia*) occurs along the edge of the reedbed (Fig. 1). Patches of reeds in the wild rice have expanded rapidly from 2006 to 2009, decreasing the distribution of wild rice. Historically, reeds were harvested for commercial use in winter.

The tidal marsh of Chongxi Wetland Research Center supports a resident population of Reed Parrotbills, which begin breeding in May and end in August–September. The Oriental Reed Warbler is resident in the area only in the summer. They migrate to the study area in April–May and leave in August–September. Reed Parrotbills feed mainly in the reedbeds and are rarely found in adjacent reed patches, in willow forests or in wild rice vegetation. Oriental Reed Warblers feed not only in the reedbeds but also in willow forests, wild rice vegetation, and adjacent farmland (LHX, pers. obs.).

Field Procedures.—In the breeding season of 2006–2007, we systematically searched the reedbed for nests of Reed Parrotbills and Oriental Reed Warblers in the study area. When an active nest was located, nest host was identified, reproduction stage was determined, brood size was recorded and the distance of nest to the edge of reedbed was measured; the nest was checked every day until all the nestlings were hatched. We used neck ligatures (plastic coated wire) to collect prey items delivered to nestlings when they were 5–8 days old. We collected provisioning items from Reed Parrotbills and Oriental Reed Warblers at the same period, i.e., from June–July of 2006 and 2007.

Prey items were identified to the lowest taxonomic level possible (see appendix) and were categorized based on taxonomic groups, flight ability, and feeding habit. The taxonomic groups used in further analyses in this study included Diptera, Hymenoptera, Coleoptera, Lepidoptera, Hemiptera, Homoptera, Orthoptera, Odonata, Araneida, Gastropoda and others. The flight ability of prey items were indexed as winged and wingless. The feeding habit of prey items were categorized as exposed (including prey items on the surface of plants or in the air) and concealed (including stem-boring insects, gall-forming fly and those feeding under leaf sheath, for example, scale insects). The relative composition of winged and wingless prey items in the diet should relate to the adult birds' flight ability, with more winged prey items in the nestling diet indicating better flight ability of the adults. The relative composition of concealed and exposed prey items in the nestling diet should relate to the adults' beak morphology with more concealed prey items in the nestling's diet indicating a stronger beak.

Statistical Analysis.—We pooled data of prey items together for each nest. The composition of nestlings' diets was calculated as the number of each prey category to the total number of prey items for each nest (proportion); frequency was calculated as the proportion of nests with each prey category.

We used the proportion of each prey category to estimate the diet breadth of each nest, using Levins' D (Levins 1968):

$$D_i = \frac{1}{\sum_j p_{ij}^2}$$

where p_{ij} is the proportion of the prey category j in nest i's provisioning items.

The diversity of provisioning items for each nest was calculated with the Shannon-Weaver index:

$$H' = -\sum p_i \ln(p_i)$$

where p_i is the proportion of the provisioning item category i's number in our records of all provisioning items of an individual nest.

We calculated the number of categories, diet breadth, and diversity of the nestlings' diet when category included only taxonomic group and category included both ecological traits (concealed-exposed, winged-wingless) and taxonomic group for both Reed Parrotbills and Oriental Reed Warblers. The proportion of concealed versus exposed prey items and winged and wingless prey items were calculated for both Reed Parrotbills and Oriental Reed Warblers.

The differences in brood size, distance of nest to the edge of reeds, total number of prey items, number of prey categories, proportions of winged, wingless, concealed and exposed prey items, diet breadth, and diversity of nestling diet between Reed Parrotbills and Oriental Reed Warblers were examined by using MANOVA with all of the above parameters as dependent variables and species as the predictor variable. The results of tests between subjects were used to show the significant differences of the above parameters between the two species.

The difference of nestling diet composition between Reed Parrotbills and Oriental Reed Warblers was examined by using MANOVA with all prey categories as dependent variables, sampling date (year and month) and species as predictor variables and distance of the nest to the edge of the reeds and brood size as covariates. We used the results of multivariate tests to show the significance differences in total nestling diet composition between Reed Parrotbills and Oriental Reed Warblers and the results of tests between subjects to show the significance differences in proportion of each prey category between Reed Parrotbills and Oriental Reed Warblers.

We performed all analyses using the SPSS statistical package software (Version 17; SPSS, Chicago, IL, USA). Data are reported in mean ± SE.

RESULTS

Sample Size and Characteristics of the Studied Nests.—A total of 81 Oriental Reed Warbler nestlings from 22 nests and 74 Reed Parrotbill nestlings from 23 nests were ligatured and had provisioning items collected. Most nests from which we collected provisioning items were located within one large reedbed (20 of 23 Reed Parrotbill nests and 21 of 22 Oriental Reed Warbler nests); three nests of Reed Parrotbills and one nest of Oriental Reed Warblers were located in patches of common reed in wild rice (Fig. 2). The brood size of the Reed Parrotbill and Oriental Reed Warbler were 3.22 (SE = 0.13) and 3.82 (SE = 0.20), respectively. The brood size of the Reed Parrotbill was significantly smaller than that of the Oriental Reed Warbler (MANOVA, $MS = 4.059$, $F = 6.420$, df = 1, $P = 0.015$). Mean distances of nest to the edge of reedbed for Reed Parrotbills and Oriental Reed Warblers were 65.65 m (SE = 10.15) and 75.86 m (SE = 11.55); and there was no significant difference between species (MANOVA, $MS = 1172.503$, $F = 0.443$, df = 1, $P = 0.51$).

Composition of Nestling Diets.—A total of 750 and 675 prey items were collected for Reed Parrotbills and Oriental Reed Warblers, respectively. The average was 32.61 (SE = 2.18) prey items for each nest belonging to Reed Parrotbills and 30.68 (SE = 2.74) prey items for each nest belonging to Oriental Reed Warblers. There was no significant difference between Reed Parrotbills and Oriental Reed Warblers in total number of prey items collected (MANOVA, $MS = 41.749$, $F = 0.306$, df = 1, $P = 0.58$).

The composition of nestling diet of the Reed Parrotbill and the Oriental Reed Warbler are summarized in Table 1 and the Appendix. The composition of delivered items was significantly different between Reed Parrotbills and Oriental Reed Warblers (MANOVA, Wilks' $\lambda = 0.023$, $F_{10, 34} = 141.372$, $P < 0.001$). The difference between species remained significant even after controlling for sampling date (year and month), the distance of nest to the edge of reeds, brood size (MANOVA, Wilks' $\lambda = 0.029$, $F_{10, 30} = 99.678$, $P < 0.001$). There were significant effects of species on proportions of most individual prey categories (Table 1), while no significant effects of sampling date (for month, all $P > 0.05$; for year, all $P > 0.05$) and the distance of nest to the edge of reeds (all $P > 0.05$). The brood size had significant effects on proportions of Araneida, Gastropoda, Hymenoptera and Orthoptera ($P = 0.012$–0.028) and no significant effects on the other prey categories (all $P > 0.05$).

Ecological Characteristics of Nestling Diets.—Comparison of ecological characteristics of nestling diets of Reed Parrotbills and Oriental Reed Warblers are presented in Table 2.

According to the flight ability of prey items, Reed Parrotbills delivered >98% of prey items that lacked wings, while ~85% of prey items delivered to nestlings by Oriental Reed Warblers had wings. According to the feeding habit of prey items, Reed Parrotbills delivered >97% of items

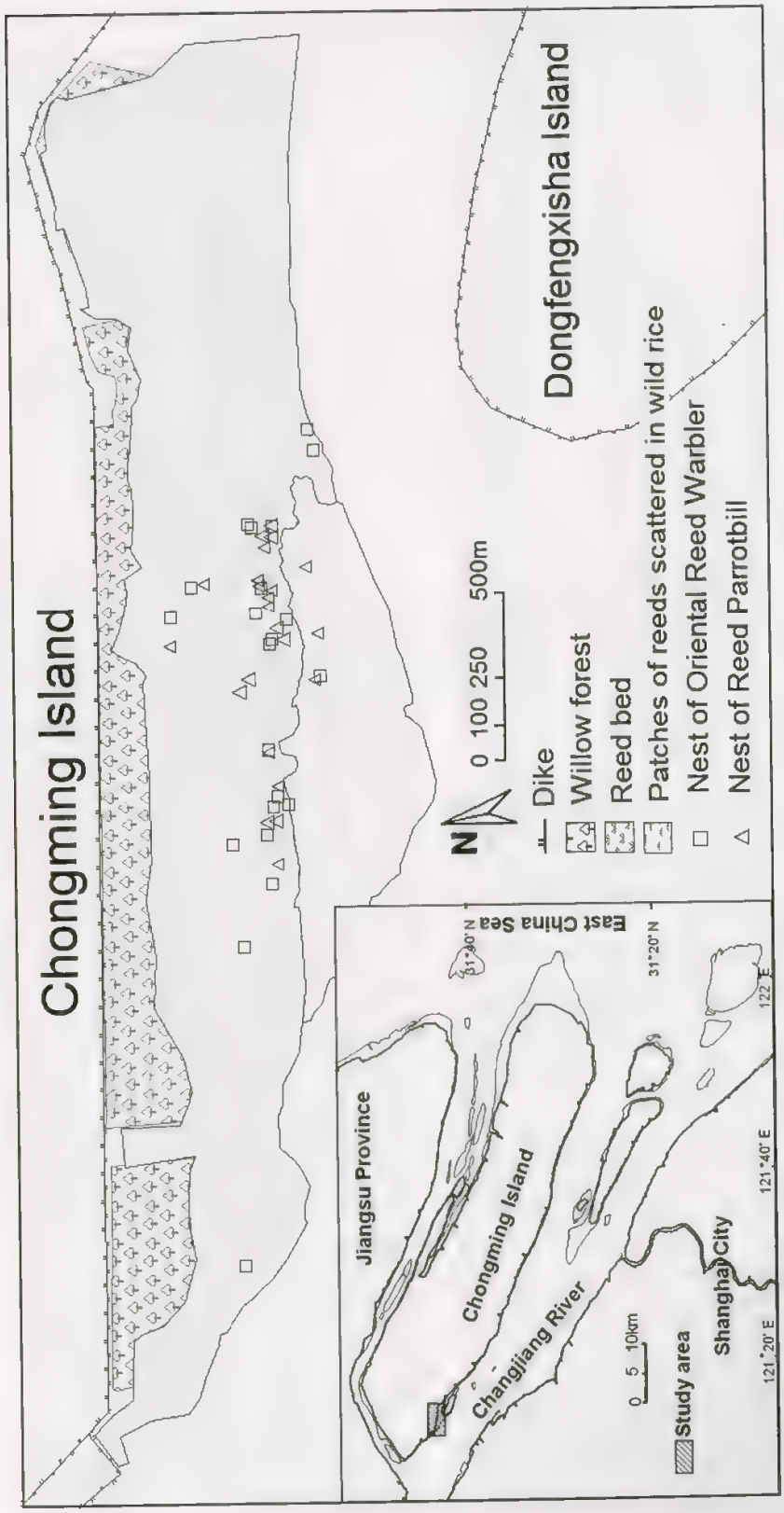

FIG. 2. Study area (Chongxi Wetland Research Center, Changjiang Estuary, China) with locations of nests of Reed Parrotbills and Oriental Reed Warblers in 2006–2007 and vegetation distribution of study area in 2006.

TABLE 1. The composition of nestlings' diet in Reed Parrotbills (RP) and Oriental Reed Warblers (ORW). Results are expressed as average of percentage of prey category to the total number of prey for each nest. Frequency is the percentage of nests where the parent birds delivered a prey item. Significance differences for individual prey category between RP and ORW after controlling sampling date (year and month), the distance of nest to the edge of reeds and brood size was examined by using MANOVA and results of between-subjects effects tests are presented. Data are shown as mean ± SE.

Taxonomic groups	RP (n = 23) % (frequency, %)	ORW (n = 22) % (frequency, %)	Tests of between-subjects effects of MANOVA (all df = 1)
Diptera	13.81 ± 1.61 (95.65)	53.05 ± 2.46 (100.00)	$MS = 1.276$, $F = 126.745$, $P < 0.001$
Hymenoptera	0.12 ± 0.12 (4.35)	17.90 ± 1.65 (100.00)	$MS = 0.342$, $F = 130.089$, $P < 0.001$
Coleoptera	0.20 ± 0.15 (8.70)	3.35 ± 0.83 (50.00)	$MS = 0.006$, $F = 7.160$, $P = 0.011$
Lepidoptera	9.37 ± 0.95 (91.30)	4.53 ± 0.86 (68.18)	$MS = 0.023$, $F = 11.761$, $P = 0.001$
Hemiptera	0.32 ± 0.18 (13.04)	1.46 ± 0.53 (36.36)	$MS = 0.001$, $F = 3.983$, $P = 0.053$
Homoptera	74.22 ± 1.89 (100.00)	2.58 ± 0.77 (54.55)	$MS = 4.358$, $F = 831.053$, $P < 0.001$
Orthoptera	0.28 ± 0.19 (8.70)	1.43 ± 0.73 (22.73)	$MS = 0.003$, $F = 5.146$, $P = 0.029$
Odonata	0.00 ± 0.00 (0.00)	0.97 ± 0.33 (31.80)	$MS = 0.001$, $F = 6.252$, $P = 0.017$
Araneida	1.20 ± 0.47 (30.43)	12.84 ± 1.71 (95.45)	$MS = 0.092$, $F = 32.032$, $P < 0.001$
Gastropoda	0.00 ± 0.00 (0.00)	1.13 ± 0.44 (27.27)	$MS = 0.000$, $F = 1.283$, $P = 0.26$
Others	0.45 ± 0.26 (13.04)	0.68 ± 0.32 (18.18)	$MS = 0.000$, $F = 0.577$, $P = 0.45$

with concealed habits, while Oriental Reed Warblers delivered >99% of items with exposed habits (Table 2). There were significant differences between the diet composition of nestling Reed Parrotbills and nestling Oriental Reed Warblers because of variability in prey flight ability and feeding habit (Table 2, both $P < 0.001$).

Reed Parrotbills delivered significantly more concealed and wingless prey items to nestlings than Oriental Reed Warblers, and Oriental Reed Warblers delivered significantly more winged and exposed prey items to nestlings than Reed Parrotbills (all $P < 0.001$).

Whether ecological traits were considered or not, Oriental Reed Warblers had significantly wider diet niche and significantly higher diversity in nestling diet than did Reed Parrotbills (Table 2).

DISCUSSION

Passerine birds must depend on both their beak and flight-related structures to efficiently exploit food resources (Price 1987, Temeles and Roberts 1993, Gosler and Carruthers 1994, Grant and Grant 1996). Beak morphology serves a critical role in feeding and is closely related to foraging ability, foraging efficiency, and dietary characteristics (Price 1987, Temeles and Roberts 1993, Gosler and Carruthers 1994, Brandl et al. 1994, Grant and Grant 1996, Radford and Du Plessis 2003). In our study, Reed Parrotbills delivered mainly wingless and concealed items to their nestlings, indicating they are limited in their ability to capture winged prey capable of strong flight and have to depend on their large beak to retrieve prey concealed within reed shoots. Oriental Reed Warblers delivered mainly exposed and winged items to their nestlings, indicating they are limited in their ability to capture prey from within reed shoots and have to depend on their flight ability to catch prey capable of strong flight. Our study demonstrated that although breeding sympatrically in reedbeds, Reed Parrotbills and Oriental Reed Warblers used different strategies in their exploitation of food resources.

In our study area, the most abundant prey items in Reed Parrotbills' nestlings were Homoptera, Dipterans and Lepidoptera, and in Oriental Reed Warblers' nestlings were Diptera, Hymenoptera, and Arachnids. In Japan, the most abundant prey item delivered to nestlings by Oriental Reed Warblers were Diptera, Araneida, Diptera and Lepidoptera (Dyrcz and Flinks 2000), and in Europe (Poland), the most abundant prey items delivered to nestlings by Great Reed Warblers (*A. arundinaceus*) were Araneida, Dipterans, Coleoptera and Lepidoptera (Dyrcz and Flinks 2000). In Europe (Poland), the most abundant prey items of Great Reed Warbler recorded by Grim (1999) were Diptera, Araneida and Hymenoptera. It appears that the main food resources used by Great and/or Oriental Reed Warblers are similar prey items to those found in reedbeds at different sites across their range.

Wide and deep beaks can apply significant bite force (Herrel et al. 2005) and allow birds to crack hard objects and reduce the risk of beak failure (Soons et al. 2010). For example, the large beaked

TABLE 2. Comparison of ecological characteristics of nestling diet between Reed Parrotbills (RP) and Oriental Reed Warblers (ORW). Significance differences for individual prey category between RP and ORW after controlling sampling date (year and month), the distance of nest to the edge of reeds and brood size was examined by using MANOVA and results of tests of between-subjects effects are presented. Data are shown as mean ± SE.

	Ecological characteristics	RP $n = 23$	ORW $n = 22$	Tests of between-subjects effects of MANOVA (all df = 1)
Composition of nestling diets according to flight ability of prey	Proportion of winged prey items (%)	1.39 ± 0.41	85.38 ± 2.02	$MS = 7.931$, $F = 1735.324$, $P < 0.001$
	Proportion of wingless prey items (%)	98.61 ± 0.41	14.62 ± 2.02	
Composition of nestling diets according to habit of prey	Proportion of concealed prey items (%)	97.42 ± 0.52	0.64 ± 0.54	$MS = 10.530$, $F = 16816.828$, $P < 0.001$
	Proportion of exposed prey items (%)	2.58 ± 0.52	99.36 ± 0.54	
Only taxonomy of prey items considered	Number of categories	3.65 ± 0.16	6.05 ± 0.40	$MS = 64.406$, $F = 31.410$, $P < 0.001$
	Diet breadth	1.73 ± 0.07	2.97 ± 0.21	$MS = 17.344$, $F = 31.717$, $P < 0.001$
	Diversity	0.76 ± 0.04	1.31 ± 0.06	$MS = 3.377$, $F = 55.466$, $P < 0.001$
Taxonomy and ecological traits of prey items considered	Number of categories	3.65 ± 0.16	6.18 ± 0.42	$MS = 71.954$, $F = 32.066$, $P < 0.001$
	Diet breadth	1.73 ± 0.07	3.00 ± 0.22	$MS = 18.201$, $F = 32.320$, $P < 0.001$
	Diversity	0.76 ± 0.04	1.32 ± 0.07	$MS = 3.530$, $F = 56.190$, $P < 0.001$

reed bunting subspecies, *Emberiza schoeniclus intermedia* can extract insect larvae from reed stems, but the small beaked, *E. s. schoeniclus* cannot (Matessi et al. 2002). In the present study, the Reed Parrotbills had significantly shorter, deeper, and wider beaks than the Oriental Reed Warblers (Fig. 1; also see Xiong and Lu 2013b). This allows Reed Parrotbills to extract prey items within the reed stems, while Oriental Reed Warblers cannot use prey items within the reed stems. In our study area, Diptera prey items used by Reed Parrotbills were mostly galls (mostly larvae or pupa of *Giraudiella* spp.), Lepidoptera were mostly stem-boring caterpillars (mostly larvae or pupa of the monophagous moth *Archanara* spp., *Phragmataecia* spp. and *Chilo* spp.) and Homoptera were mostly scale insects (*Nipponaclerda biwakoenesis*). These prey items have concealed feeding habit: scale insects settle on reed shoots under a leaf sheath, gall makers protrude inward from the internode wall of reed shoots and stem-boring caterpillars consume the inside of shoots (Wang et al.1989). Concealed prey items consisted of more than 97% of the nestling Reed Parrotbills' diets, but only <1% of the Oriental Reed Warblers', indicating that beak morphology constrained the Oriental Reed Warbler to use prey items within reed stems. The difference in diet composition based on the feeding habits of prey items between Reed Parrotbills and Oriental Reed Warblers likely is the result of differences in beak morphology.

Flight performance also relates to food type (Marti 1974, Andersson and Norberg 1981). To catch prey items capable of strong flight, a bird must also be capable of strong flight. Oriental Reed Warblers in our study area delivered mainly winged prey items (>85%), which is consistent with studies in Japan and Poland (Grim 1999, Dyrcz and Flinks 2000), while Reed Parrotbills delivered mainly wingless prey items (>98%), indicating that Oriental Reed Warblers are better in flight than Reed Parrotbills. This may also reflect differences in flight morphology between migratory and sedentary birds; the Oriental Reed Warbler is a migratory bird and the Reed Parrotbill is a sedentary bird. It appears that their flight ability has limited Reed Parrotbills to use primarily winged prey items. Their high performance in flight allows Oriental Reed Warblers to exploit food and nest material resources not only in the reedbeds but also in the surrounding vicinity (Dyrcz and Flinks 2000, Xiong and Lu

2013b). Our field observations found that feeding grounds of Oriental Reed Warblers include both reedbed and the surrounding vicinity, such as willow forest, wild rice vegetation, and adjacent farmland, while feeding grounds of Reed Parrotbills include only reedbeds and rarely patches of reeds in wild rice and willow forests (LHX, pers. obs.). Thus, Oriental Reed Warblers had significantly more taxonomic categories in their diet, wider diet niche, and higher diversity in diet than Reed Parrotbills (Table 2).

In conclusion, flight ability appears to limit Reed Parrotbills' use of winged prey items, while beak morphology compensates for their limitation in flight ability by facilitating their use of prey items with concealed habits. In contrast, the beak morphology constrains the Oriental Reed Warblers' use of prey items with concealed habit, while their flight ability allows them to use winged prey items capable of strong flight. Thus, Reed Parrotbills and Oriental Reed warblers have evolved different strategies to exploit the different food resources available in reedbeds. Reed Parrotbills are a highly-specialized species, able to use resources not available for other small passerines associated with reeds, and this ability likely allows them to winter in reedbeds or close to breeding areas.

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APPENDIX. Characteristics and composition of nestling diets of Reed Parrotbills and Oriental Reed Warblers collected in June and July of 2006 and 2007 in the Chongxi Wetland Research Center, Changjiang Estuary, China.

				Reed Parrotbill		Oriental Reed Warbler	
Taxa/species	Age	Flight ability	Feeding-habit	Number	Frequency	Number	Frequency
Araneida							
Araneae							
Clubionidae							
Clubiona spp.	adult	wingless	exposed	6	0.17	47	0.82
Lycosidae							
Pardosa spp.	adult	wingless	exposed	4	0.17	16	0.41
Tetragnathidae							
Tetragnatha spp.	adult	wingless	exposed			26	0.64
Gastropoda							
Stylommatophora	adult	wingless	exposed			9	0.27
Insecta							
Coleoptera							
Cerambycidae	adult	winged	exposed			6	0.18
Coccinellidae	adult	winged	exposed	2	0.09	23	0.45
Diptera							
Calliphoridae	adult	winged	exposed			109	0.86
Cecidomyiidae							
Giraudiella spp.	larva/pupa	wingless	concealed	100	0.96	3	0.05
Cecidomyiidae	adult	winged	exposed			69	0.77
Muscidae	adult	winged	exposed			176	0.95
Hemiptera							
Anthocoridae	adult	winged	exposed			4	0.18
Nabidae	adult	winged	exposed	3	0.13	6	0.23
Homoptera							
Aclerdidae							
Nipponaclerda biwakoensis	adult	wingless	concealed	562	1.00		
Aphididae	adult	winged	exposed			3	0.14
Cicadellidae	adult	winged	exposed			8	0.36
Delphacidae	adult	winged	exposed			5	0.14
Hymenoptera							
Braconidae							
Apanteles spp.	adult	winged	exposed			12	0.41
Elasmidae	adult	winged	exposed			28	0.73
Ichneumonidae	adult	winged	exposed	1	0.04	71	0.91
Lepidoptera							
Noctuidae							
Archanara spp.	larva/pupa	wingless	concealed	52	0.87		

APPENDIX. Continued.

Taxa/species	Age	Flight ability	Feeding-habit	Reed Parrotbill		Oriental Reed Warbler	
				Number	Frequency	Number	Frequency
Noctuidae	adult	winged	exposed			8	0.32
Pyralidae							
Chilo spp.	larva/pupa	wingless	concealed	4	0.09		
Pyralidae	adult	winged	exposed			5	0.18
Zeuzeridae							
Phragmataecia spp.	larva/pupa	wingless	concealed	11	0.35	4	0.09
Zeuzeridae	adult	winged	exposed			19	0.55
Odonata							
Libellulidae	adult	winged	exposed			8	0.32
Orthoptera							
Conocephalidae	adult	winged	exposed	2	0.09	3	0.14
Locustidae							
Locusta spp.	adult	winged	exposed			3	0.14
Others	adult	winged	exposed	3	0.13	4	0.18

Note: Prey items were collected using neck ligatures from 81 Oriental Reed Warblers nestlings from 22 nests and 74 Reed Parrotbills nestlings from 23 nests. The frequency was calculated as the proportion of nests delivered with each prey category.

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UNUSUAL WINTERING DISTRIBUTION AND MIGRATORY BEHAVIOR OF THE WHOOPING CRANE (*GRUS AMERICANA*) IN 2011–2012

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ABSTRACT.—The last, self-sustaining population of Whooping Cranes (*Grus americana*), the Aransas-Wood Buffalo population, has overwintered almost exclusively along the Gulf Coast of Texas, USA, in and around the Aransas National Wildlife Refuge during recent decades. In late autumn and winter 2011–2012, Whooping Cranes were observed several hundred kilometers from coastal wintering grounds, with at least 13 Whooping Cranes in central Texas, south-central Kansas, and central Nebraska from November 2011 to early March 2012. Notably, family groups of Whooping Cranes were observed around a Texas reservoir, Granger Lake, over a 3-month period. An extreme drought, coupled with record warm temperatures in the southern and central United States, may have interacted to influence behaviors and distributions of Whooping Cranes during winter 2011–2012. Such observations suggest that Whooping Cranes may be more opportunistic in use of wintering habitat and/or more likely to re-colonize inland historical sites than previously thought. Continued documentation of Whooping Cranes overwintering in areas other than the Texas coast and/or altering timing of migration will be important for protection and management of additional winter habitat as well as for informing population estimates for the Aransas-Wood Buffalo Population of Whooping Cranes. *Received 6 May 2013. Accepted 15 August 2013.*

Key words: Aransas National Wildlife Refuge; Cheyenne Bottoms State Waterfowl Management Area, Kansas; climate; Granger Lake, Texas; Platte River, Nebraska; Quivira National Wildlife Refuge, Kansas; Whooping Crane; wintering habitat.

The Whooping Crane (*Grus americana*) is one of the most endangered species of birds in North America and the world (National Audubon Society 2006, IUCN 2012). The last wild, self-sustaining population of Whooping Cranes, the Aransas-Wood Buffalo population (AWBP), migrates more than 3,800 km from Wood Buffalo National Park, Canada, to in and around Aransas National Wildlife Refuge (NWR), Texas, USA, and has rebounded from fewer than 20 individuals in the early 1940s (Allen 1952) to over 250 individuals in 2011–2012 (Strobel et al. 2012). This population expansion represents tremendous improvement, but the species remains far from meeting recovery goals, which include the AWBP numbering above 1,000 individuals if two additional wild, self-sustaining flocks of Whooping Cranes cannot be established (CWS and USFWS 2007). A key factor in the recovery of Whooping Cranes is provision of adequate habitat across the species' range, including wintering grounds.

Historically, Whooping Cranes wintered in prairies, marshes, and coastal lagoons throughout southwestern Louisiana, the Gulf Coast of Texas, the Rio Grande Delta in northeastern Mexico, as well as inland grasslands, including the tablelands of west-central Texas and the high plateaus of central Mexico (Stevenson and Griffith 1946, Allen 1952, CWS and USFWS 2007). Overharvesting of Whooping Cranes and habitat loss and degradation led to precipitous declines in Whooping Cranes by the end of the 19th century (McIlhenny 1943, Allen 1952). By the time Aransas NWR was created in 1937, its lands encompassed nearly all of the wintering range of the remaining migratory Whooping Cranes (Stevenson and Griffith 1946, Allen 1952). As the AWBP increased over subsequent decades, locations of winter territories expanded to surrounding marshlands, and territory sizes decreased, permitting more birds to occupy coastal areas in and around Aransas NWR, including nearby Matagorda Island (Stehn and Johnson 1987), an area that Whooping Cranes used prior to their decline (Allen 1952). Occasionally juvenile Whooping Cranes have been observed elsewhere during winter, such as a juvenile in Oklahoma and Kansas in 1987 (Stehn 1992), a juvenile in Oklahoma and Nebraska in 2008–2009 (Stehn 2009), and a juvenile near Medford, Oklahoma, in 2009 (Stehn 2010). However, most Whooping Cranes have remained concentrated within the brackish marshes of the Gulf Coast during recent winters.

Such a small, isolated population within a limited geographic area is vulnerable to stochastic events (Mills 2007), such as chemical spills along the Gulf Intracoastal Waterway and hurricanes that could decimate the population (CWS and

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USFWS 2007). Changing climatic and environmental conditions may further negatively influence availability of fresh water and associated food resources for Whooping Cranes (CWS and USFWS 2007, Chavez-Ramirez and Wehtje 2012). Collectively, such factors threaten the long-term viability of the species, and the future of Whooping Cranes may depend, in part, on dispersal of the core population from current wintering grounds to other suitable areas within the historical winter range.

During winter 2011–2012, family groups of Whooping Cranes were observed away from the Texas Gulf Coast for the first time in recent history. Birds were far beyond the sampling frames for the U.S. Fish and Wildlife Service Wintering Whooping Crane Abundance Survey (Strobel et al. 2012). Observers did, however, record locations and behaviors of Whooping Cranes in these unusual areas in a variety of formats, including internal agency notes and electronic discussion lists. Herein we summarize winter 2011–2012 sightings and discuss implications of this expanding winter distribution of Whooping Cranes.

METHODS

We contacted personnel from the U.S. Army Corps of Engineers, U.S. Fish and Wildlife Service, and Kansas Department of Parks and Wildlife, as well as searched LISTSERV sites (KSBIRD-L 2012, Texbirds LISTSERV 2012) for summaries of reported sightings of Whooping Cranes in atypical wintering areas from November 2011 to March 2012. Site-specific information was compiled and evaluated to eliminate redundant data points, and when possible, more than one source was contacted to ensure validity of observations. We conservatively summarized observations. In several cases birds likely were present for longer periods, but we present only sightings reported with daily records of location. We included descriptions of habitats occupied when such details were available through photographic documentation or reported by observers.

RESULTS

Whooping Cranes were observed hundreds of kilometers away from typical wintering grounds during winter 2011–2012 (Fig. 1), with birds at Granger Lake, a reservoir in central Texas (Williamson County); at Quivira National Wildlife Refuge in south-central Kansas (Stafford County); near Cheyenne Bottoms State Waterfowl Management Area in central Kansas (Ellsworth County); and along the Platte River in central Nebraska (Dawson County).

Whooping Cranes were most commonly reported from Granger Lake, with sightings spanning mid-November 2011 through early March 2012, and as many as nine birds seen on some occasions (Fig. 2; Texbirds LISTSERV 2012; JDC, unpubl. data). The first sighting at Granger Lake was on 14 November, when observers saw four Whooping Cranes in flight from the dam. The next report came on 21 November when a flock of three birds, composed of two adults and one juvenile, was feeding in a cornfield near the lake. One week later, two adults and one juvenile were in an agricultural field near the lake, and a single family group of the same composition was observed three more times 3–6 December. On 7 December two family groups were reported, both containing two adults and one juvenile. From 7 December 2011 until 2 February 2012, Whooping Cranes were seen regularly, and multiple observers documented three and six individuals during this time. Then, on 7 February 2012, an observer saw nine Whooping Cranes congregated in an area immediately north of Granger Lake, where six birds previously had been observed. Nine individuals were seen multiple times at or near Granger Lake until 19 February 2012, and six individuals were reported on 3 March 2012. Personal observations (JDC, pers. obs.) and photographs revealed that Whooping Cranes were associated with agricultural fields, grazed pastures, depressional wetlands, and dammed ponds around Granger Lake.

Up to six Whooping Cranes were reported on some occasions at Quivira NWR from 19 November 2011 to 24 January 2012 in marsh habitats (Fig. 2; KSBIRD-L 2012; B. A. Jones, pers. comm.). On 19 November, a single Whooping Crane was observed with a large group of Sandhill Cranes (*G. canadensis*) near Quivira NWR, and a single Whooping Crane was reported daily through 27 November. A single Whooping Crane again was reported on 5 December, and an individual was reported daily until 19 December in the same area. Additional sightings at Quivira NWR included four Whooping Cranes on 24–25 November, three on 7 December, and six on 24 January 2012 (Fig. 2).

Three Whooping Cranes, two adults and one juvenile, were reported from private land near

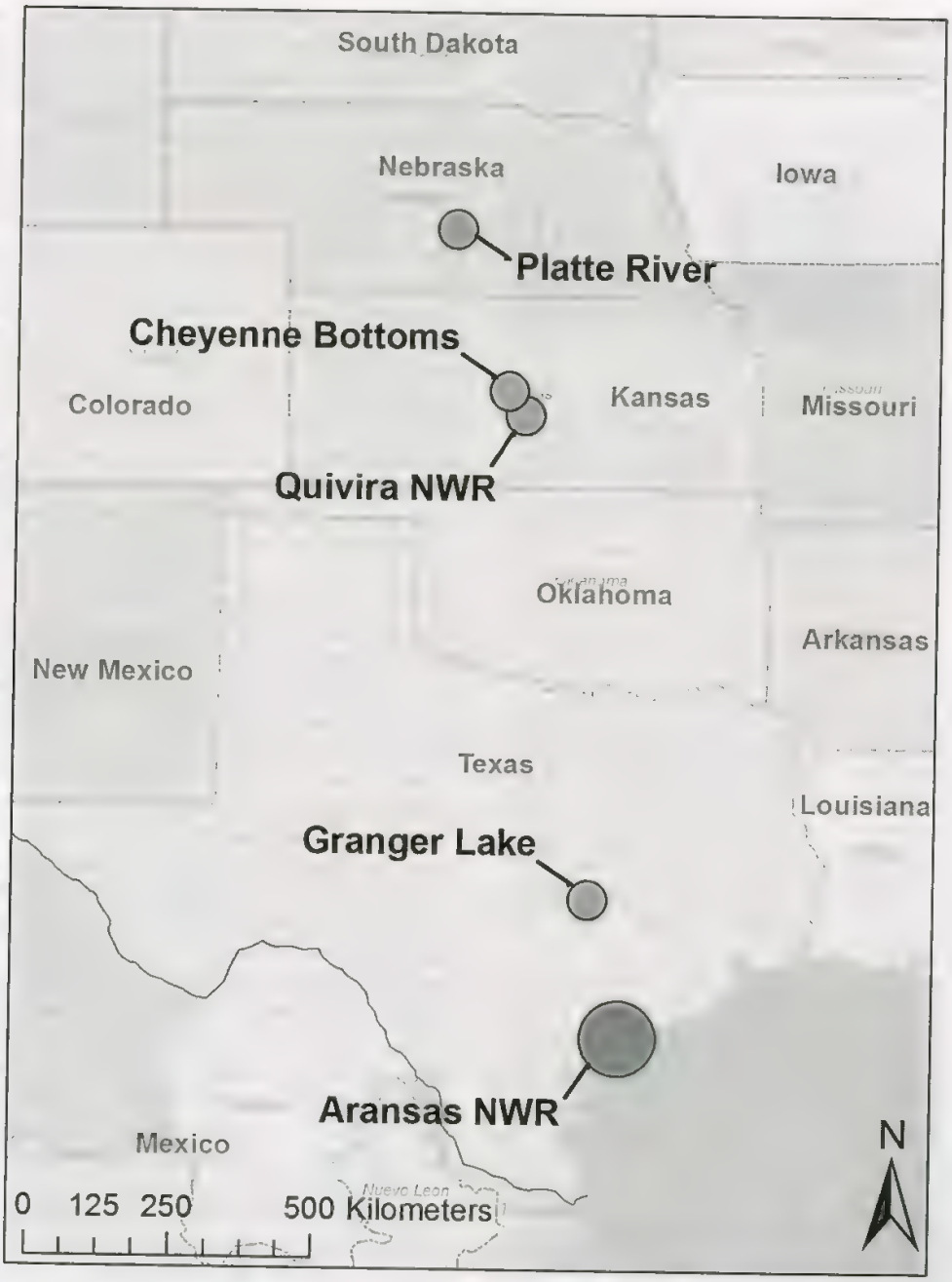

FIG. 1. Locations of reported Whooping Cranes mid-November 2011 through mid-February 2012. Large circle denotes their primary wintering area along the Texas Gulf Coast in and around the Aransas National Wildlife Refuge (NWR), and small circles indicate additional sites occupied by Whooping Cranes during winter of 2011–2012.

Cheyenne Bottoms State Wildlife Area from late November 2011 to mid-January 2012 (Fig. 2). A family group was seen from 23 November to 13 December 2011 (K. E. Grover, pers. comm.). Additional information obtained from a listserv accounted for three birds multiple times from 14 December to 24 January 2012 (KSBIRD-L 2012). The birds likely were present between reported observations, as the sightings are from the same location and of the same flock composition, but

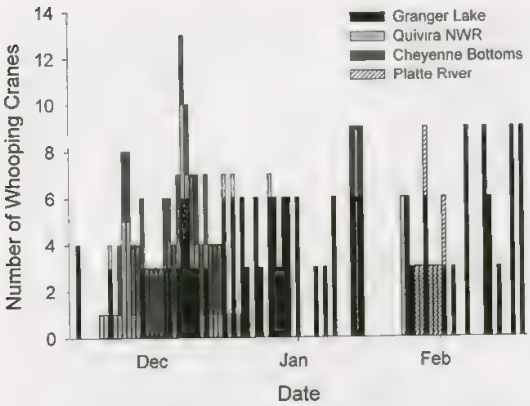

FIG. 2. Number of confirmed sightings of Whooping Cranes outside of the Texas Gulf Coast mid-November 2011 through mid-February 2012. Additional sightings were reported through early March 2012, but these later observations were excluded from the figure, because they may have been birds initiating early migration.

only specific dates recorded are depicted in Figure 2.

On 27 January 2012, three Whooping Cranes, two adults and one juvenile, were confirmed within the main channel of the Platte River near Jeffery Island in Overton, Nebraska (M. C. Tacha, pers. comm.). The Whooping Cranes last were seen on the Platte River on 2 February 2012. On 4 February 2012, heavy snow and strong north winds impacted the area; the birds were not re-sighted after the storm.

DISCUSSION

It is difficult to disentangle whether Whooping Cranes were overwintering, extending migration, or exhibiting some combination of these behaviors during winter 2011–2012, but it is clear that large numbers of Whooping Cranes, notably family groups, were away from Aransas NWR during the typical overwintering period. The winter of 2011–2012 was the fourth warmest on record for the United States (NOAA 2012), and Texas experienced exceptional drought during the months when Whooping Cranes typically overwinter along the Gulf Coast (U.S. Drought Monitor 2012). In addition to the unusual distribution of Whooping Cranes, Sandhill Cranes were far north of typical wintering grounds, with several thousand along the Platte River in central Nebraska during winter 2011–2012 (MJH, unpubl. data), providing further evidence that mild conditions in the central United States were favorable for cranes during winter months.

A number of interacting factors likely contributed to the unusual distribution of Whooping Cranes in 2011–2012. During autumn 2011 migration, Whooping Cranes may have lingered at stopover sites because of warmer conditions and availability of open, unfrozen water, either delaying arrival at Aransas NWR or terminating migration at more northerly sites. Alternatively, Whooping Cranes may have reached Aransas NWR and subsequently departed, possibly because of poor habitat conditions associated with the drought or overcrowding linked to an expanding population. Some cranes might have traveled between sites and/or initiated extremely early migration, such as the Whooping Cranes along the Platte River in late January. Historically, few Whooping Cranes have been documented migrating before late March, except in 2010 when individuals were observed in Oklahoma in late February and early March (Stehn 2010). Off-refuge sightings of Whooping Cranes in 2012 were considerably earlier than previous records, suggesting that some individuals were overwintering rather than migrating—especially the Granger Lake birds.

Three of the non-coastal sites occupied by Whooping Cranes during winter 2011–2012 were within or adjacent to areas designated as critical habitat for migrating Whooping Cranes (Platte River, Cheyenne Bottoms, Quivira NWR; USFWS 1978). Granger Lake is not an area identified as critical habitat, but it lies within the migratory corridor and likely serves as a short-duration stopover site. The region surrounding Granger Lake is moderately developed, populated, and bisected by multiple roads (JDC, pers. obs.). Because of these factors and publicity generated by these Whooping Cranes in 2011–2012, it is unlikely that more have wintered around Granger Lake in recent times. Whooping Cranes did, however, inhabit this inland region during the mid-19th century, with records of "immense flocks" of Whooping Cranes in Williamson County during spring 1884 and Whooping Cranes as a "favorite game fowl" and "an abundant winter resident" in nearby McLennan County (Stevenson and Griffith 1946 and references therein). Therefore, the individuals at Granger Lake might have been re-occupying an historical-use area, even though the natural habitat has been altered from a riverine landscape to its

current condition as a flood-control reservoir. Alternatively, the current habitat conditions of the drawn-down reservoir may have attracted the birds during migration.

The condition of Granger Lake and surrounding lands provided resources conducive to multiple-month occupancy by Whooping Cranes in winter 2011–2012. Granger Lake is a reservoir on the San Gabriel River in Texas owned and managed by the U.S. Army Corps of Engineers for flood control, water supply, and recreation. The reservoir was impounded in 1980 and has experienced extreme siltation over the last three decades. Under normal conditions, the lake covers approximately 1,800 ha and has a relatively shallow depth averaging 3 m, with inter-annual water-level fluctuations <1 m (JDC, unpubl. data). The lake reached an all-time low on 9 November 2011, exposing many sand bars and mud flats, as well as numerous crayfish and bivalves (JDC, pers. obs.). This decline in lake level coincided with the autumn migration of Whooping Cranes through Texas, and birds frequently were observed foraging around the reservoir margin until lake levels rose >1 m by late February 2012, once again submerging mud flats. The great (at least nine birds) and extended use (three months) suggest that the reservoir and surrounding lands provided suitable conditions during a drought for Whooping Cranes to acquire resources necessary for survival during winter. These observations warrant further investigation to understand how fluctuating water levels of reservoirs influence use by Whooping Cranes throughout the entire migratory corridor, as well as whether there are any negative effects of exposed sediments on the birds, such as detected for Sandhill Cranes along a depleted reservoir in New Mexico, USA (DeRagon et al. 2005).

Collectively, these unusual distributional patterns suggest that Whooping Cranes may be much more flexible in selection of wintering habitat than previously described, and this plasticity might be essential to the growth of the population outside of Aransas NWR as demand for wintering habitat increases. It is likely that other areas exist in Texas and surrounding states that could provide adequate resources to wintering Whooping Cranes, if birds have a way to gain knowledge of those sites. The successful reintroduction of Whooping Cranes in the eastern United States (CWS and USFWS 2007), as well as their historical distribution (e.g., Allen 1952), illustrates the species' potential to occupy diverse habitats during winter. However, the current paradigm of wintering habitat conservation for AWBP focuses on the preservation and creation of favorable coastal habitats immediately adjacent to areas already occupied by Whooping Cranes in and around Aransas NWR (CWS and USFWS 2007). Documentation of overwintering site use and behavior—especially far from the Gulf Coast—will inform population estimates for Aransas-Wood Buffalo Whooping Cranes and help guide protection and management of wintering habitat over a larger area. Such documentation also may allow us to monitor interactions between wild and reintroduced Whooping Cranes should their habitats eventually overlap. To facilitate this, ongoing efforts will be needed to increase public awareness about reporting observations of Whooping Cranes, as well as to systematically document and validate off-refuge sightings during winter.

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THE LIFE OF ALEXANDER WILSON

Alexander Wilson was born on 6 July 1766 in Paisley, Scotland. At age 12 he was writing poetry and soon after became an apprentice weaver. Later as a journeyman he alternately wove and roamed the Scottish countryside peddling his cloth. In 1790, Wilson published his first book of poems, soon followed by a second, and still later by the wildly popular "Watty and Meg," a variation on *The Taming of the Shrew*. At the birth of the industrial revolution, young Wilson supported the weavers with a series of stinging poems that revealed the injustices of the mill owners. He soon found himself in court facing charges of blackmail and libel. The charges were allowed to sleep, but never decided. Consequently Wilson left Scotland to settle near Philadelphia. There he taught school, met William Bartram, America's foremost naturalist, and conceived the *American Ornithology*. From 1803 to his death in 1813, Alexander Wilson traveled over 12,000 miles, visited all 15 states and 4 territories of the United States, discovered 26 species of birds, wrote and illustrated 314 accounts of birds of eastern North America, sold 450 subscriptions, and edited and supervised publication of the nine volume *American Ornithology*. In honor of the 200th anniversary of Wilson's achievement, we will be running a series of short stories on Alexander Wilson and the making of American ornithology.

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Short Communications

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Time Budgets of Male Calliope Hummingbirds on a Dispersed Lek

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ABSTRACT.—Several authors have suggested that male Calliope Hummingbirds (*Selasphorus calliope*) perform their dive and shuttle displays on "dispersed leks" where the dramatic aerial displays of several individuals can be seen or heard from a single location. To expand on the limited information available on breeding territorial behavior, I provide detailed time budget data from 3 years of observation of males in a 20-year-old seed-tree cut in Montana. Males spent the vast majority of their time (76%, on average) perched on dead willow branches that extended upward to 4–5 m in height, and an average of 90% of perch time was spent at no more than three perch sites. Most of the rest of the males' time (15%, on average) was spent off territory, where they conducted a good portion of their feeding. About 6% of a male's time was spent performing energetically demanding dive and shuttle displays, which were directed primarily toward females, but also toward other bird species perched within the male's territory. Displays directed toward females were sometimes followed by copulation while she was perched. This is only the second geographic location where male Calliope Hummingbirds are reported to have congregated in what appears to be a dispersed lek. We still know little about how common the clustering of breeding territories is, whether such clustering is limited to early successional habitat, and whether relatively few males obtain most of the copulations in such clusters, as would be expected in a classic lek breeding system.
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Key words: Calliope Hummingbird, dispersed lek, disturbance, dive display, shuttle display, wildfire.

Although male Calliope Hummingbirds (*Selasphorus calliope*) are known to defend territories during the breeding season (Ryser 1985, Calder and Calder 1994), breeding territorial behavior cannot be explained in the context of food-resource defense because defended areas contain few to no available food resources. Moreover, there are often nearby undefended areas that harbor a considerable abundance of profitable flowers (Tamm 1985, Armstrong 1987, Powers 1987). After conducting food-availability manipulation studies, Armstrong (1987) concluded that breeding territories probably provide males with non-energetic benefits of reproductive success with females who, in much the same way that any lek-breeding female might, visit and choose to mate with one or more of the displaying males. Both Armstrong (1987) and Tamm et al. (1989) suggested that because territories are relatively small but spaced apart, the males may be positioning themselves in an "exploded lek" (hereafter referred to as a dispersed lek) where the dramatic aerial displays of several individuals can be seen or heard from a single location (Höglund and Alatalo 1995). Whether Calliope Hummingbirds perform dramatic aerial displays in this manner outside the single study area in British Columbia where Tamm (1985), Armstrong (1987), and Tamm et al. (1989) worked is unknown because of the absence of similar studies elsewhere.

Here, I compare the behavior of male Calliope Hummingbirds on breeding territories in Montana with that of males in British Columbia. To describe how several male Calliope Hummingbirds used their time while they occupied display territories, I collected time budget data from 11 territories across three breeding seasons within a 20-year-old seed-tree cut in western Montana. An additional study of the breeding behavior of this hummingbird species is timely because there is growing concern about pollinators in general and about reported declines in hummingbird populations. In reference to the Calliope Hummingbird, the National Audubon Society (2013) reports nonsignificant declines rangewide, but significant declines in Montana and Oregon. Although the scientific basis for negative population trends is not strong, it is certain that we need to better understand the biology and needs of Calliope Hummingbirds in order to design conservation measures that might benefit the species.

METHODS

Study Site.—I obtained observations from eight territories within a mixed-conifer forest on U.S. Forest Service land about 8 km southeast of

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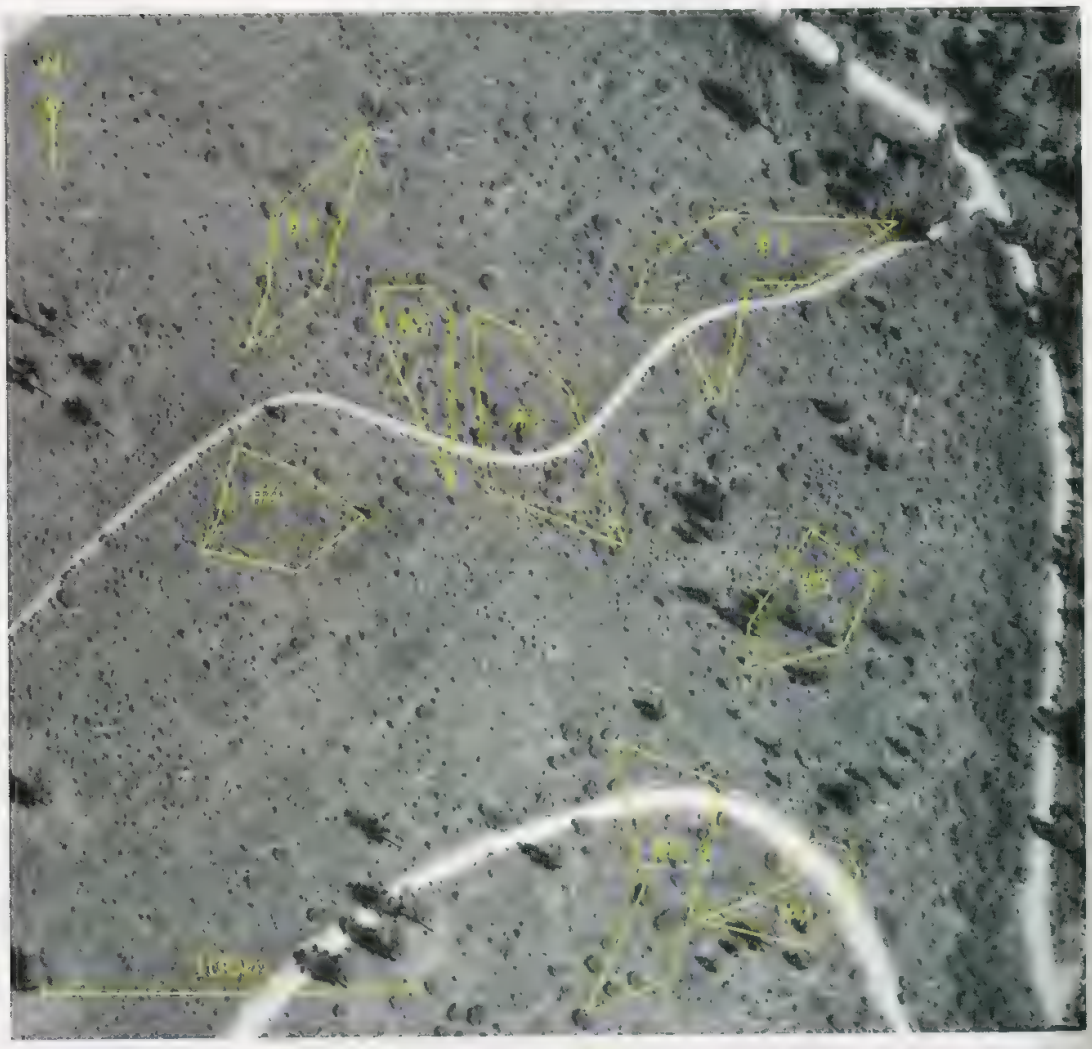

FIG. 1. Aerial view of the main study site located 8 km southeast of Missoula, Montana. Lines connect perch sites used by a single bird in any breeding season. The enclosed areas (averaging ~0.1 ha each) were defended against other males, but because little feeding occurred within the boundaries shown, these represent breeding territories that were used primarily to attract and display to females before copulation.

Missoula, Montana (46.8191° N, 113.9361° W) during the month of June in 1983, 1984, and 1985. This 10-ha site had undergone a seed-tree harvest about 20 years before the study began, and it was bisected by a small dirt road and bordered by a small stream to the north and east. Two additional territories were located in 1985 in a nearby forest patch (46.8163° N, 113.9556° W) that had burned severely 8 years earlier, and was subsequently used in a companion study in 1989 (Leider 1990). Both sites consisted of a mixture of ponderosa pine (*Pinus ponderosa*), western larch (*Larix occidentalis*), and Douglas-fir (*Pseudotsuga menziesii*). In both sites, mature trees were widely scattered and the shrub component was well developed (Fig. 1). The tall shrub layer was dominated by Scouler's willow (*Salix scouleriana*); the remaining shrub species included Saskatoon serviceberry (*Amelanchier alnifolia*), Rocky Mountain maple (*Acer glabrum*); mallow ninebark (*Physocarpus malvaceus*), Woods' rose (*Rosa woodsii*), russet buffaloberry (*Shepherdia canadensis*), common chokecherry (*Prunus virginiana*), and sticky currant (*Ribes viscosissimum*).

Territory Mapping and Time Budgets.—I used an aerial photograph (1 cm = 15.6 m) of the study

site taken in 1983 so that I could trace every visible shrub, tree, and downed log onto notebook paper that I then used in the field to label individual perch sites that were used by a focal individual. By observing individual unmarked birds continuously, I was able to construct territory boundaries by plotting the convex polygon that circumscribed the series of perches used by a particular individual (Fig. 1). In any given year, I observed individuals on 5–7 different territories, and observed 1–4 birds on any given day between the hours of 0700–2000 Mountain Daylight Time (MDT). Individual birds were not marked, but my ability to track individuals from perch to perch and the consistency in use of perches within a given year makes it likely that the activity record for a given territory in a given year represented the activity of a single individual.

The time associated with each of a series of possible hummingbird activities was recorded with a stopwatch in continuous bouts that lasted from 20–90 mins. Activities included: (1) perch, where a bird was stationary on a perch site that was identified through the use of a lettering scheme on the map, (2) fly, where a bird was watched during continuous horizontal flight, (3) hover, where a bird was flying above a single point in space outside the context of a dive display, (4) disappear/feed, where a bird either disappeared from sight or was observed to feed from flowers, (5) chip-chip threat flight, where a bird chased another bird (usually another male hummingbird) while giving rapid "chip-chip-chip-chip" calls as it pursued the other bird, (6) dive display, where a bird ascended to a height of 20–30 m before diving toward the ground in a U-shaped trajectory that resulted in a loud "bzzzt-zeee" sound produced by the tail feathers and syrinx, respectively, at the bottom of the dive, and (7) shuttle display, where a bird hovered in front of another bird or plant part while rotating from side to side with the tip of the beak in a fixed forward position (shuttling back and forth) and produced what sounds a lot like the buzzing noise that a bumblebee makes in the process of sonication or buzz-pollination.

Ortiz-Crespo (1980), Stiles et al. (2005), Clark (2011a, 2011b), and Clark et al. (2012) provide more detail, video, and sound recordings of the two displays described above. Clark and his colleagues have described how the tail feathers and the syrinx are each involved in sound production during dive displays (Clark 2011a, Clark et al. 2011a), and how the wings produce noise during a shuttle display, which appears to be common to all "bee" hummingbird species.

While on breeding territories, males routinely direct dive and perform shuttle displays toward females and other bird species that intrude; in contrast, males engage in aggressive territorial defense by vocalizing, chasing, and (rarely) diving at intruding males (Tamm et al. 1989). The dive and shuttle displays are, therefore, primarily courtship displays, although males may direct dive and shuttle displays toward other perched birds.

Statistical Analyses.—Whether the same individuals used the same perch sites from one year to the next is unknown because the birds were unmarked. In another study (Tamm et al. 1989), three of five banded male Calliope Hummingbirds returned to the same territories in the second year of study, suggesting that some of the males in the present study probably also returned to the same territory in multiple years. Therefore, to be statistically conservative, I assumed that the individual on any given territory from one year to the next was the same, and I used each territory (across years) as a sample unit for the calculation of means. I used a generalized linear modeling approach to test for differences in the mean percentage of time that a target bird spent in different activities and for interactions between the distribution of time among activities and bird or year. I used observation bouts of 30 successive activities to calculate the mean percentages of time spent in each activity for any given bird (I subsampled from longer observation bouts to determine that 30 successive activities generally produced means that changed little with the addition of more time). I used an ANOVA to test whether the mean number of dives differed significantly among objects of dive display, and a chi-square test to investigate whether the number of times a particular activity followed another kind of activity was greater than expected because of chance alone.

RESULTS

For any given bird, the percentages of time spent in each of the seven activity categories differed significantly among activity types ($P < 0.001$), with the vast majority of time (76%, on average) spent perched (Fig. 2). The next most time-consuming activity (15%, on average) belonged to the disappear/feed category, and because at least some of that time can be safely

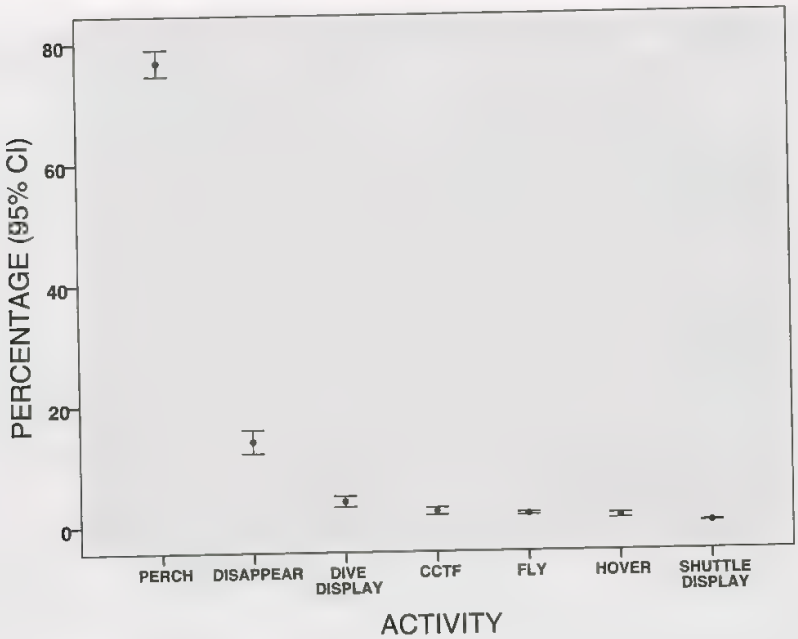

FIG. 2. Mean percentages of time that each of 11 males spent in each of the seven activities shown (CCTF = chip-chip threat flight). Bars represent 95% confidence intervals, which reveal how similar the relative percentages were among male territories. The vast majority of a male's time was spent perched on just a few upward-pointing bare willow branches.

attributed to travel and use of rarely used perch sites that I may have overlooked, a given male probably spent no more than 10% of his time feeding. This is identical to the percentage of time that male Calliope Hummingbirds spent feeding at a site in British Columbia (Armstrong 1987). Males fed from the flowers of a variety of plant species (*Castilleja miniata, Lonicera ciliosa, Penstemon cyaneus, Ribes viscosissimum, Rosa woodsii,* and *Amelanchier alnifolia*) both on and off territory; females were observed on rare occasion to feed on a male's territory. Because of the direction of some flights where I lost sight of a bird, I also suspect that several males visited feeders at a house that was about 300 m south of the nearest territory. Nearly 6% of a bird's time was spent in dive displays, and the rest in other forms of flight. The distribution of time among activities did not differ among years, but did differ among males (Wald $\chi^2 = 17.8$, df = 12, $P < 0.01$ for the interaction between bird and activity). Though significant, those differences were small enough that the overall distribution of time among activities was still strikingly similar among males (Fig. 2).

Perch Sites.—An individual male used an average of 5.5 (range = 2–10) different perch sites on his territory in any given season, but an average of 90% of a bird's perch time (range = 61.2–100%) was accounted for by summing the time spent on only three different perches. The vast majority of perch sites used by males in this seed-tree cut were the dead tips of upward-pointing willow branches that were 4–5 m in height. Of the 68 different perch sites distributed among the eight territories situated in the seed-tree cut site, 47 (69%) were dead willow branch tips. The only other kind of perch sites used were tops of Douglas-fir, ponderosa pine, or western larch seedlings (26%), and short extensions of wood atop broken-top snags (5%). The total time spent on the different perch site types was even more heavily tilted toward the use of upward-pointing dead willow branches (79.9% of total perch time). As Armstrong (1987) noted, elevated perch sites are key elements in male Calliope Hummingbird territories.

Territories.—Individual territories were about 0.1 ha in size (range = 0.06–0.12 ha), and they were not contiguously distributed (Fig. 1). The sizes and spacing of territories are strikingly similar to the six territories that Armstrong (1987) mapped in his study. Most of the perch sites used by an individual on a particular territory from one

TABLE 1. A list of the species and the number of instances that they were "objects" of a variety of males' dive displays (objects were positioned directly beneath the bottom of the display arc). All but male Calliope Hummingbirds were also sometimes the object of a shuttle display that followed a series of dives (they were approached to within a few centimeters by a male performing a shuttle display).

Object of dive	Frequency	Percent	Mean # dives
unknown	110	NA	2.4
female Calliope Hummingbird, *Selasphorus calliope*	32	26.0	5.1
Chipping Sparrow, *Spizella passerina*	26	21.1	3.2
Dusky Flycatcher, *Empidonax oberholseri*	20	16.3	2.5
Warbling Vireo, *Vireo gilvus*	19	15.4	3.3
Orange-crowned Warbler, *Oreothlypis celata*	5	4.1	2.2
Dark-eyed Junco, *Junco hyemalis*	4	3.3	3.3
male Calliope Hummingbird, *Selasphorus calliope*	3	2.4	2.0
American Robin, *Turdus migratorius*	3	2.4	3.7
MacGillivray's Warbler, *Geothlypis tolmiei*	2	1.6	3.0
Black-headed Grosbeak, *Pheucticus melanocephalus*	2	1.6	2.0
Cassin's Finch, *Haemorhous cassinii*	1	0.8	-
chipmunk, *Tamias* sp.	1	0.8	-
Cedar Waxwing, *Bombycilla cedrorum*	1	0.8	-
Swainson's Thrush, *Catharus ustulatus*	1	0.8	-
Mountain Chickadee, *Poecile gambeli*	1	0.8	-
Pine Siskin, *Spinus pinus*	1	0.8	-
House Wren, *Troglodytes aedon*	1	0.8	-
Mean	233	100.0	3.0

year to the next were the same, so territory boundaries were similar from one year to the next.

Time Budgets.—I observed male hummingbirds during morning (before noon) and (rarely) evening hours for a total of 42.7 hrs over the course of the 3-year study. The total time an individual was watched varied from 1–6 hrs, but the resulting activity budgets were remarkably similar among individuals, with the vast majority (70–80%) of their time spent perching and most of the rest of their time off territory, where they must have conducted most of their feeding (Fig. 2). Of the 175 dive display bouts observed, disappear/feed was the next activity observed in 48 instances (27.4% of the time) and it was one of the next two activities in 83 instances (47.4% of the time). Because I observed a total of 3,258 separate activities, the probability of a disappear/feed bout following a randomly selected activity was 0.116 (175/3258). Thus, feeding was significantly more likely to be the very next ($\chi^2 = 38.3$, df = 1, $P < 0.001$), or one of the next two ($\chi^2 = 183.4$, df = 1, $P < 0.001$) activities following a dive display than one would expect because of chance alone.

Dive Displays.—I observed a total of 232 dive displays by males, and when I had a clear view of the display, there was invariably an identifiable "object" located slightly below the bottom of the dive where the male produced the "bzzzt" tail-feather sound. Dive displays were most often elicited by the presence of another bird perched within the owner's territory. Of the 123 displays where I could identify an object of display, female Calliope Hummingbirds were the most frequent objects (26%), followed by a variety of other bird species and, on one occasion, a chipmunk (Table 1). The large number of objects of dive displays (15 bird species and a mammal) adds to what has been previously documented (Tamm et al. 1989, Calder and Calder 1994). Together, Chipping Sparrow (*Spizella passerina*), Dusky Flycatcher (*Empidonax oberholseri*), and Warbling Vireo (*Vireo gilvus*) made up 61% of the 232 displays, whereas other male Calliope Hummingbirds constituted only 2.4% of the displays. Tamm et al. (1989) recognized three kinds of responses to an intruder and found that females and other passerines received a dive display 100% and 85% of the time, respectively, whereas males received a dive display only 5% of the time and a chase 95% of the time that they intruded on a territory. Although not broken down by species in their table, Tamm et al. (1989) specifically mentioned *Empidonax* sp., Nashville Warbler (*Oreothlypis ruficapilla*), and Chipping Sparrow as passerine objects of display in their study area in British Columbia.

A dive display consisted of an average of 3.0 dives, and the number of dives was significantly (ANOVA, $F = 5.6$, df = 9, $P < 0.001$) larger for females (5.1) than for other objects of display. Tamm et al. (1989) also found the number of dives toward females to be between two and three times the number involved in displays directed toward other objects. Displays directed toward females were also often interspersed with hovering, where the male descended slowly before either continuing with a few more dives or descending to directly in front of a female where he performed a shuttle display with his open bill pointed directly at the female. On six occasions when copulation was observed, each time it was preceded by a shuttle display. As Tamm et al. (1989) reported, shuttle displays were sometimes directed at other species, or toward leaves or twigs; shuttle displays were conducted within 3 cm of both a Chipping Sparrow and a Dusky Flycatcher, neither of which moved in response.

DISCUSSION

The breeding territorial behavior of male Calliope Hummingbirds is strikingly similar between the locations in British Columbia and Montana where detailed time budget data have been collected, and the behavior comes close to satisfying the four criteria set by Bradbury (1981) for defining lek behavior: (1) male parental care is absent; (2) territories contain few to no food resources needed by females; (3) males aggregate at a site, the lek or arena, to display to females while being separated by a few meters or less; and (4) females choose among males for mating purposes and may elect not to mate. In classical leks, females obtain no resources aside from the male's gametes from within a male's territory, but in dispersed leks, males maintain large enough territories that females may forage and even nest within a male's territory (Bradbury and Gibson 1983, Foster 1983, Armstrong 1987, Gibson and Bradbury 1987, Powers 1987, Höglund and Alatalo 1995, Hingrat and Saint Jalme 2005). The observations of displaying males described here reveal that the 0.1-ha territories were not contiguous, but they were still close enough that one could see and/or hear multiple males at the same time. Display arenas, such as the one described here for Calliope Hummingbirds, are, therefore, probably best defined as dispersed leks, where females may secure a limited supply of food, but where the primary resource appears to be the male himself. This was the conclusion drawn by Armstrong (1987) and Tamm et al. (1989) on their study site in British Columbia. Just how common these sorts of display arenas are in the breeding biology of Calliope Hummingbirds is unclear, but the only studies involving detailed time budgets of males on territories during the breeding season (Armstrong 1987, Tamm et al. 1989, Leider 1990, and this study) have now each reported a remarkably similar phenomenon.

Males spend 76% of their time perched, and most of the remaining time feeding. Because observed feeding bouts were usually coupled with the bird disappearing for a period before returning to a known perch, I lumped feeding with "disappear" to unknown locations. The latter probably involved travel to and feeding from food sources outside the defended area, perhaps travel to and feeding at homes with feeders, or travel to and perching at sites that I missed. The total disappear/feed time, therefore, represents the maximum amount of time that a bird could have spent feeding, so something less than that (perhaps no more than around 10% of a male's time) is spent feeding. Interestingly, the disappear/feed category followed soon after the dive display category much more often than one would expect due to chance, suggesting that feeding occurs when a bird disappears from view and that, for energetic or other reasons, displays may stimulate a refueling bout by males.

Male Calliope Hummingbirds in the two Montana study sites performed dive and shuttle displays precisely as described elsewhere (Tamm 1985, Tamm et al. 1989, Clark 2011b). The dive and shuttle displays of the Calliope Hummingbird appear to be used in a manner that is very similar to the way the Rufous Hummingbird (*Selasphorus rufus*) uses the same components of its territorial display. Clark et al. (2011b) report that most shuttle and dive displays by Volcano (*Selasphorus flammula*) and Scintillant (*Selasphorus scintilla*) hummingbirds were directed toward females, and Hurly et al. (2001) also found that dive and shuttle displays performed by Rufous Hummingbirds were directed primarily toward females, while chasing usually accompanied intrusion by males. Thus, breeding territoriality in *Selasphorus* hummingbirds appears to be a display-oriented phenomenon. Very similar descriptions of congregations of males in what appear to be dispersed leks have now been confirmed in two distant locations and two kinds of open vegetation types,

but we still know little about how common the clustering of breeding territories is and whether relatively few males obtain most of the copulations, as would be expected for true lek behavior.

The vegetation types within which male Calliope Hummingbirds establish territories in western forested landscapes has also received little formal research attention, although it is generally believed that males occupy primarily openings like meadows and disturbance-induced early successional habitat created by timber harvest or wildfire (Powers 1987, Sallabanks et al. 2006), whereas females choose nest sites in dry conifer forests, aspen, and streamside riparian areas adjacent to the more open areas used by males (Pitelka 1942, Tamm 1985, Armstrong 1987, Tamm et al. 1989, Leider 1990). Indeed, data from point counts conducted in the USFS Northern Region between 1992–1994 (n = 7,281; Hutto and Young 1999), and from the more recent 20-year database (n = 61,478; USFS Northern Region, unpubl. data) show that the probability of detecting a Calliope Hummingbird in vegetation types classified as streamside shrublands (where mostly females were detected) and early successional shrublands following moderate to heavy timber harvest or wildfire (where mostly males were detected) is around 2%, which is 3–4 times greater than the overall average. More important, nowhere are they more abundant than in those particular vegetation types (Calder and Calder 1995, Hutto and Young 1999). Both Calliope and Rufous hummingbirds, therefore, depend to a certain extent on ephemeral, early successional habitat created by natural or human-caused disturbance, but we know nothing about how restricted their display arenas are to these vegetation types, nor do we know anything about whether birds using naturally versus artificially created openings do equally well in terms of survival or reproductive success. As Calder and Calder (1994) emphasize in their birds of North America account, we have only begun to scratch the surface of important questions surrounding the breeding biology of this iconic western hummingbird.

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Feeding Rates, Double Brooding, Nest Reuse, and Seasonal Fecundity of Eastern Wood-Pewees in the Missouri Ozarks

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ABSTRACT.—Despite being widespread and abundant, little is known about the breeding ecology and natural history of the Eastern Wood-Pewee (*Contopus virens*), in part because nests are often high in the canopy, difficult to view, and adults are monomorphic. We monitored nests of Eastern Wood-Pewees and recorded the feeding rate of nestlings by adults as part of a larger study on breeding demography of Eastern Wood-Pewees across a gradient of savanna, woodland, and forest in the Missouri Ozarks in 2010–2011. We monitored 287 nests between 26 May and 22 August and conducted feeding rate observations for 54 nests with nestlings. There was an 88-day nesting season with peaks of nest activity on 24 June and 22 July. We recorded 19 cases of double brooding and nine cases of within-season nest reuse. Seasonal fecundity was 2.2 fledglings per territory. The frequency of parental feeding visits increased with nestling age. These are additional observations of nest reuse, nesting cycle lengths, and breeding season length for Eastern Wood-Pewees; future demographical research of marked individuals will continue to fill in gaps in breeding ecology for this common and widespread flycatcher.
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Key words: breeding ecology, double brooding, Eastern Wood-Pewee, feeding rate, Missouri Ozarks, nest reuse, seasonal fecunditv.

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Eastern Wood-Pewees (*Contopus virens*; hereafter "pewee") are vocal and abundant Neotropical migrant songbirds that breed in a variety of wooded habitats across the eastern United States north into the southern regions of Canada (McCarty 1996). Because pewees are abundant across a range of habitats, we can observe them to evaluate effects of forest disturbance and management on demographics such as productivity. Several studies evaluating abundance and nest survival in relation to forest management have included pewees (Davis et al. 2000; Knutson et al. 2004; Brawn 2006; Grundel and Pavlovic 2007a,b; Newell and Rodewald 2011, 2012), but, with the exception of Newell et al. (2013), studies have not focused on pewee breeding ecology. Thus, there are large gaps in our knowledge of their natural history possibly because of an inability to easily reach high nests, which average 18 m in the Missouri Ozarks (range: 2.6–26.6 m, n = 310; Kendrick et al. 2013). Our objective was to acquire additional knowledge of the demographics of Eastern Wood-Pewees including nesting dates, number of nest attempts, breeding season length, and parental feeding rates, because these demographic data are lacking in the literature. Feeding rate data are important common measures of parental behavior (Taylor and Kershner 1991, Darveau et al. 1993, Whitehead and Taylor 2002, Altman and Sallabanks 2012), and the frequency of parental nest

visits may affect nest predation (Martin et al. 2000). Nesting dates, number of nest attempts, and occurrence of double brooding are important parameters for estimating species productivity and population viability (Donovan and Thompson 2001, Etterson et al. 2011). Here we report our observations of nesting dates of pewees, nest attempts and double brooding, nest reuse, and parental feeding rates collected as part of a larger study on pewee demography in savanna, woodland, and forest in Missouri (Kendrick et al. 2013).

METHODS

Study Area.—We studied pewees in the Ozark Highlands of Missouri. The region is equally divided between steep and rolling hills, and gently rolling plains (McNab and Avers 1994). The region includes oak (*Quercus* spp.)-hickory (*Carya* spp.) and oak-hickory-pine (*Pinus echinata*) forest, bluestem (*Andropogon gerardii*, *Schizachyrium scoparium*) prairie, and eastern redcedar (*Juniperus virginiana*) glades (McNab and Avers 1994). We selected 13 sites across the region on lands owned by the Missouri Department of Conservation, the Missouri Department of Natural Resources, The Nature Conservancy, and the U.S. Department of Agriculture Forest Service. More information on site selection and the characteristics of savanna, woodland, and forest sites can be found in Kendrick et al. (2013).

We began this research as part of a study investigating the response of breeding birds to savanna and woodland management in 2009, but intensified and focused our efforts on pewees in 2010 and 2011 (Kendrick et al. 2013). We searched for pewee nests between early May and mid-August using parental behavior within a territory. Nests were monitored every 3–4 days, or daily near predicted fledge date, to determine if nests were active, the stage of the nest, and nest contents. We constructed a telescoping video pole that included a Spiderbeam antenna pole (WiMo; Herxheim, Germany) and a wireless camera and monitor (Defender Phoenix surveillance system; Defender, Niagara Falls, Ontario) to view nest contents up to 16.5 m high. A team of two people used the pole to determine nest contents once per nest stage (i.e., incubation and nestling stages). Lay and hatch dates were estimated based on observations from video pole checks, parental behavior, and nestling size. We did not use the video pole if we detected Blue Jays (*Cyanocitta cristata*), American Crows (*Corvus brachyrhynchos*), or Brown-headed Cowbirds (*Molothrus ater*) to minimize time at the nest and attention drawn to the nest. We considered a nest to be successful if we verified at least one host fledgling. We attempted to locate a re-nesting attempt for a pair in a territory when a nest failed. In 2010, we focused on observing parental behavior of pewees to locate and monitor nests, distinguish territories, and monitor pairs throughout the breeding season; in 2011, we intensified our effort by monitoring territories with successful nests to determine if pairs attempted second broods. We did not uniquely color-band birds, but by closely monitoring territories and the timing of nest fates, and witnessing removal of nest material from failed nests to build second nests, we believe we accurately detected re-nesting and double brooding attempts.

We used the modified productivity model of Farnsworth and Simons (2001, 2005) to estimate seasonal fecundity. Model assumptions are: (1) clutch size is constant for all nests, (2) a female nests as many times as possible if time remains in the breeding season, (3) daily nest survival is constant throughout the breeding season and between stages, (4) all eggs hatch and all young fledge in successful nests, (5) no adult mortality occurs in the breeding season, and (6) the time it takes an adult to initiate a re-nest attempt does not vary (Farnsworth and Simons 2001). We only used data from nests in 2010 and 2011 for the nesting parameters reported here because of increased effort in these years to monitor number of attempts and nest contents; however, the daily nest survival value for the productivity model was taken from Kendrick et al. (2013) and is based on all monitored nests 2009–2011 (n = 310).

We measured feeding rate by observing nests across a range of nestling ages for 1 hr between sunrise and 1200 CST in 2010 and 2011. We recorded the arrival time and duration of every visit made by either adult, and we recorded number of nestlings in the nest. We also observed behavior at the nest (e.g., if the parent brooded nestlings after feeding). We fit a general linear model to determine the effects of nestling age and number of nestlings on the number of feeding visits/hr; because only three of 39 observations of feeding rate were repeat observations on the same nest, we did not account for repeated visits in the model with an additional covariance term.

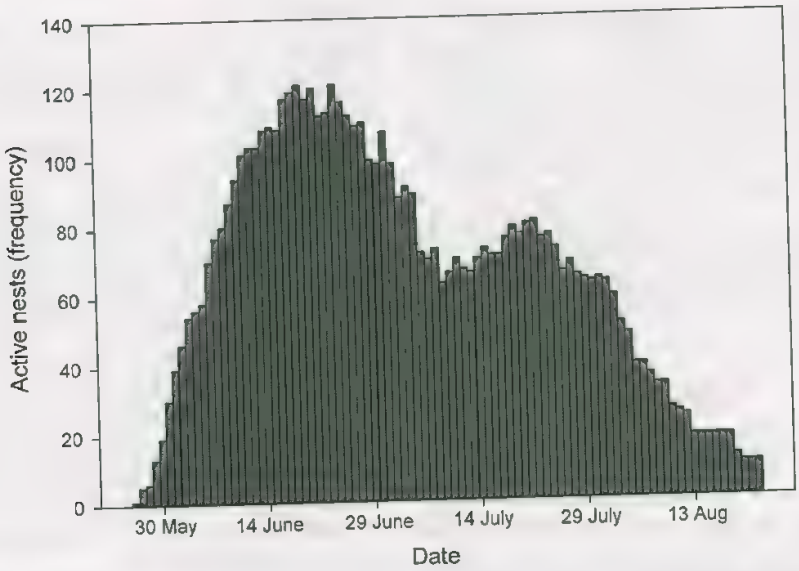

FIG. 1. Frequency of active nests of Eastern Wood-Pewees by date for nests found in the Missouri Ozarks, 2010–2011.

RESULTS

We monitored 69 and 217 nests in 2010 and 2011, respectively. The earliest active nest we observed (probably in laying stage) was 26 May and latest active nest was 22 August (Fig. 1), similar to breeding season dates for pewees in Ohio (Newell et al. 2013). The greatest number of active nests for 2010 and 2011 pooled was on June 24 with a secondary peak on July 22; the breeding season lasted 88 days (Fig. 1). Based on 70 successful nests found in the building stage, we estimated the mean length of the nesting cycle from the beginning of a clutch to fledging was 33.5 days (SE = 0.31), including 14.1 days (SE = 0.42) for the incubation stage and 15.4 days (SE = 0.46) for the nestling stage.

We observed multiple nesting attempts after failure; 53 pairs attempted a second nest and five attempted a third nest. We documented an average of 8.15 days (SE = 0.6; n = 34) between nest failure and the first egg of a re-nesting attempt. We never observed pewees reusing a nest after a failure. Of 92 territories that successfully fledged young in 2011, 19 (21%) attempted a second brood but only three were successful. We documented an average of 9.4 days (SE = 0.92; n = 14) between a successful nest and the first egg of a re-nesting attempt. One of the 19 pairs made three unsuccessful attempts for a second brood, thus four nest attempts was the maximum we observed for any territory. Nine pairs reused their first successful nest for a second brood attempt, but none of these were successful.

We observed both adults tending to fledglings in the immediate nest area even after the second nest was active. We observed adults adding material to nests that had previously fledged young before laying another clutch. Not all second broods were initiated early in the season; the latest double brood attempt was found early in the incubation stage on 1 August. Because we monitored nests at different sites every year, we were unable to examine whether pewees reused nests in subsequent years. For pairs that did not reuse nests, mean distance between the first successful nest and second nest was 42.7 m (range: 23.54–72.56 m; n = 9).

We estimated seasonal fecundity to be 2.2 fledglings per female based on the Farnsworth and Simons model (2001, 2005). The seasonal fecundity estimate was based on a daily nest survival of 0.98 (95% CI: 0.97–0.98, n = 310; Kendrick et al. 2013), an average clutch size of 2.6 (n = 110; Kendrick et al. 2013), a maximum of four nesting attempts per female per breeding season, a maximum of two broods per female per breeding season, a 100% probability of re-nesting after nest failure if enough time remained in the breeding season, and an average of 2.2 fledglings per successful nest (n = 64; Kendrick et al. 2013) in

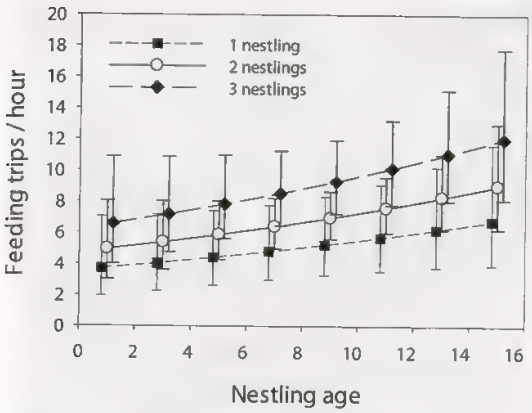

FIG. 2. Effect of nestling age on the frequency of adult feeding visits to the nest by Eastern Wood-Pewees in the Missouri Ozarks, 2010–2011.

addition to the nesting parameters reported above to estimate seasonal fecundity.

We recorded parental feeding visits for 54 nests with nestlings ranging in age from 1–15 days. Mean feeding rate was 8.03 visits/hr (SE = 0.61) and mean duration of nest visits was 1.32 min (SE = 0.22). We modeled effects of nestling age and number of nestlings on a subset of 39 nest observations for which we knew the number of nestlings. A negative binomial distribution was more suitable than a Poisson or normal distribution; there was no evidence of lack of fit of the model based on the overdispersion parameter ($\hat{c}$ = 1.07). The number of nestlings and nestling age had marginally significant effects (P = 0.062, P = 0.11; respectively) and feeding visits increased with more nestlings and older nestlings (Fig. 2). We could not determine feeding rates by sex, because we did not color-band adults, but we did confirm both adults feeding at the nest individually (observed when parents switched places at the nest to feed) and simultaneously. We observed adults sitting on nestlings that were up to 8 days old after feeding.

DISCUSSION

We located and monitored a large sample of nests and determined pewees made up to four nest attempts; we documented additional instances of double brooding and multiple cases of within-season nest reuse (Newell et al. 2013), and calculated the first known estimate of seasonal fecundity for the Eastern Wood-Pewee in the Missouri Ozarks. Basic demographic data such as breeding season and nesting cycle lengths from a large sample have not been previously reported for the pewee. Old accounts from a handful of nests report an incubation period of 12–13 days and a nestling stage of 15–18 days (Bent 1942), both period lengths within about 1 day of our findings. The pewee nesting cycle of 33.5 days includes a laying stage of ~4 days. We previously documented a mean clutch size of 2.6 (range: 1–3; n = 111; Kendrick et al. 2013). Some flycatchers have been found to lay one egg per day (Oppenheimer et al. 1996); thus, our estimate of a laying stage length of ~4 days may be a slight overestimation.

The number of attempts we reported is determined from the minimum number of nest attempts made, because we are not confident we found every attempt made for each pair. For example, a nest found later in the breeding season in a territory without any previous documented attempts is difficult to report as a second or third attempt when we may not have found previous nest attempts. Acadian Flycatchers (*Empidonax virescens*) will sometimes make up to five re-nesting attempts after a failure (Whitehead and Taylor 2002). Nest reuse in subsequent years has been reported for pewees (Bent 1942), and nest reuse between years also occurs in Western Wood-Pewees (*Contopus sordidulus*; Bent 1942, Curson et al. 1996). Benefits of within-season nest reuse may include less time and energy that pewees must spend searching for new nest locations and materials (Curson et al. 1996), whereas drawbacks include increased nest predation (Lima and Dill 1990) and potential nest failure because of structural damage (Bergin 1997). Structural damage may be less of a concern for within-season nest reuse than reuse in subsequent years. While individuals were not color-banded, we believe that we observed double brooding based on nest reuse, observed territory boundaries, known nesting status of neighboring territories, removal of material from previous nest attempts for the construction of another nest, and parental care of fledglings that remained in the territory while a second nest was initiated.

Basic information on clutch size, number of young fledged, and re-nesting attempts allowed us to calculate an estimate of seasonal fecundity, which is a key component of population models. Our estimate of 2.24 is similar to the 2.03 and 2.23 fledglings per female for monogamous and polygynous pewees, respectively, in Ohio (Newell

et al. 2013). Our estimated fecundity was also similar to a seasonal fecundity of 2.5 for Acadian Flycatchers (Fauth and Cabe 2005) and previous-season fecundity of 2.27 for territory-faithful female Willow Flycatchers (*Empidonax traillii*; Sedgwick 2004). As expected, feeding rates increased with nestling age. Increased activity at the nest during the nestling stage may explain higher predation rates observed during the nestling stage (Kendrick et al. 2013). Feeding rates in Ohio (Newell et al. 2013) were almost twice those we observed, but mean brood size was similar, so it is unclear what is driving this difference or what the consequences are. Different provisioning rates could reflect subtle differences in methodologies between studies or different prey quality or availability and could result in differences in nestling condition or size; however, we did not measure nestlings.

We report demographic information about Eastern Wood-Pewees to contribute to our understanding of the species and Neotropical migratory birds in general. We provided information on the occurrence of double brooding and seasonal fecundity of pewees; knowledge of both of these aspects of breeding biology is limited for Neotropical migrants (Faaborg et al. 2010). We think future research to address remaining gaps in breeding biology should include marking adults to enable identification of individuals and a better understanding of parental roles and singing behavior of males and females as well as other aspects of demographics such as survival.

ACKNOWLEDGMENTS

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New Caledonian Crows' (*Corvus moneduloides*) Pandanus Tool Designs: Diversification or Independent Invention?

Gavin R. Hunt[1]

ABSTRACT.—New Caledonian Crows (*Corvus moneduloides*) manufacture the most complex foraging tools used by nonhuman animals. Not only do they shape multiple tool designs of different complexity out of raw material using distinct, design-specific manufacture techniques, they are the only species to incorporate hook technology. The three different hook tool designs that they cut out of barbed *Pandanus* spp. leaves are suggested to have evolved by a process of diversification through cumulative changes rather than independent invention. Here, I describe three examples of an oversized version of the so-called 'narrow' pandanus tool design in an area where narrow tools are also made. My observation of the way a crow used one of these oversized tools in the wild suggests that they may be efficient for foraging in especially deep probe sites. The co-occurrence of two different designs originating from a very similar manufacture technique is consistent with diversification. Furthermore, qualitative data suggest that shape variation in the three previously described pandanus tool designs might be associated with ecological function. These findings strengthen the possibility that pandanus tool designs are an example of rudimentary diversification developed in close association with functional requirements. *Received 16 May 2013. Accepted 5 November 2013.*

Key words: *Corvus moneduloides*, cumulative change, design diversification, New Caledonian Crow, pandanus tools, tool manufacture, tool use.

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New Caledonian Crows (NC crow; *Corvus moneduloides*) manufacture complex foraging tools because they shape distinct tool designs out of raw material that incorporate hook technology (Hunt 1996, Hunt and Gray 2002, 2004a, b). One material that they use to do this is *Pandanus* spp. (screw pine) leaves. The crows manufacture three distinct hook-tool designs from the barbed edges of these leaves: wide tool, narrow tool and stepped tool designs (Hunt and Gray 2003). Variation in the shape of each design mostly exists between sites, with a high degree of shape consistency within individual sites (Hunt and Gray 2003). The shape variation within both the uniformly broad wide tool and narrow tool designs is mostly to do with tool length. More complex shape variation exists among stepped tools because the characteristics of the tapered edge vary as well as tool length (e.g., the number and spacing of steps).

The manufacture of a pandanus tool can be inferred from inspecting missing sections of leaf edge on *Pandanus* spp. trees. The shape of a pandanus tool precisely matches the shape of the missing leaf edge associated with its manufacture (this missing edge is usually referred to as a 'counterpart'; Hunt and Gray 2003). Identifying a counterpart of the completed manufacture of a pandanus tool is not always straightforward. Wide

FIG. 1. Four examples of narrow strips ripped by NC Crow(s) and left hanging from the leaf edges of a *Pandanus* sp. tree. The green strip in the foreground is the only living one; the others are brown and will eventually drop off the tree. The decay process does not leave the characteristic wisp of fiber that often remains after narrow tool manufacture. These four strips were on a tree where only narrow tool manufacture had been carried out.

tool and stepped tool manufacture is relatively easy to detect from bill cuts at both ends of the missing leaf edge. Also, unfinished manufacture attempts are uncommon, and if they occur the uncompleted tool is likely to remain intact on the leaf edge because the width of the cut strip prevents decay. The situation with narrow tools is different for reasons that are unclear. In areas where narrow tools are made and used, NC crows commonly rip narrow strips of leaf edge and then leave them hanging from the leaf (Fig. 1) (Hunt and Gray 2003; GRH, pers. obs.). These hanging strips decay much more readily and consequently most probably fall off the leaf, thus making it problematic to identify successful narrow tool manufacture. Nonetheless, obvious cuts at both ends of a narrow strip of missing leaf edge clearly indicate the completed manufacture of a narrow tool.

Lack of any recapitulation in the techniques to make each of the three pandanus tool designs demonstrates that the designs are distinct. To make both a stepped tool and a wide tool an experienced NC crow first rips leaf edge away from the trunk before ripping towards the trunk to

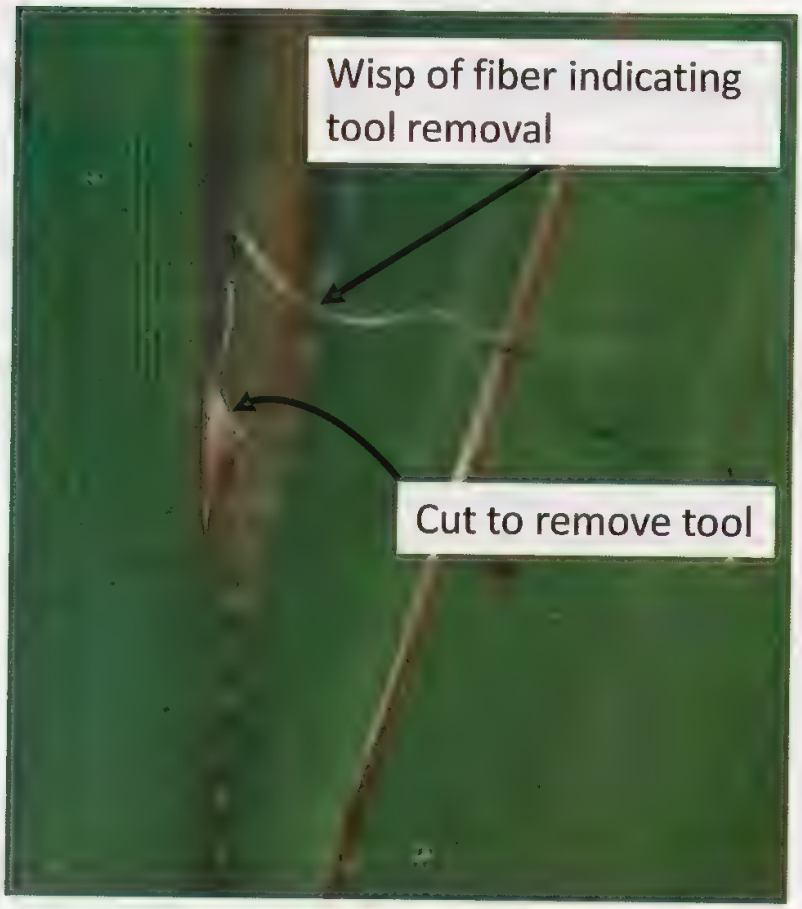

FIG. 2. Characteristics of the removal of a narrow pandanus tool from the barbed edge of a *Pandanus* sp. leaf. The cut and associated wisp of fiber indicates that the ripped strip was cut and pulled off the leaf by an NC crow. Note that the width of the leaf edge removed is the width generally observed for narrow pandanus tools (up to several mm).

remove the tool (Hunt and Gray 2004b, Holzhaider et al. 2010). However, forming the tapered section of a stepped tool is a distinctly different and more complex process than the relatively quick and simple cut-rip action that begins wide tool making. In contrast to the other two designs, the initial rip to make a narrow tool is towards the trunk. This can be inferred from the relatively high occurrence of uncompleted manufacture where ripped strips of leaf edge are left hanging from leaves. The final cut to remove the tool is made just before the ends of these hanging strips and can often be detected from close inspection of relatively recent counterparts. This is because the cutting and pulling action involved frequently leaves a short wisp of leaf fiber on the counterpart (Fig. 2); the presence of a wisp is a consequence of an NC crow not fully cutting the ripped strip before pulling it off the leaf. A wisp of fiber on a counterpart is not a characteristic of wide tool manufacture (GRH, pers. obs.). This feature is probably present because the removal cut is made before the end of the rip (e.g., as in Fig. 2), whereas the final cut to remove a wide tool is commonly made after the end of a rip (Holzhaider et al. 2010).

A crucial question is what mechanisms and processes are responsible for the multiple, standardized pandanus tool designs that sometimes co-occur at the same location (e.g., all three described designs are made in Parc Rivière Bleue in the southeast of mainland Grande Terre; Hunt and Gray 2003). In early human stone tools, such artefactual evidence has been explained by design diversification through cumulative changes driven by ecological adaptation (Stout 2011). Different types of tools made by common chimpanzees

FIG. 3. (A, B) Pandanus tool counterparts RB19 and RB89 collected along the Rivière Bleue, Grande Terre, in 2005 (A: length = 46.7 cm; maximum width of removed tool = 1.2 cm, minimum width of removed tool = 0.5 cm; B: length = 41.2 cm; maximum width of removed tool = 0.7 cm, minimum width of removed tool = 0.6 cm). Both counterparts were on the left edge of their respective leaves. A distinct wisp of fiber indicating that the cut to remove the tool from the leaf was proximal to the trunk is present on the right end of counterpart B. No wisp is present on counterpart A, but examination of cuts at each end suggests that the cut for tool removal was also proximal to the trunk. (C) A pandanus tool collected from an NC crow along the Rivière Bleue in 2005 shown below its counterpart (tool length = 49.2 cm). The counterpart was on the right edge of a leaf. A fine wisp of fiber is present on the left end of the counterpart, indicating that the cut for tool removal from the leaf was proximal to the trunk. Note the two cuts to begin manufacture at the right end of the tool and at the left end of counterpart A.

(*Pan troglodytes*) are associated with task-specific needs, including tool sets for extracting termites (Sanz et al. 2010). These tool sets consist of heavier tools for initially breaking apart mounds and the subsequent use of finer tools for extracting the termites. However, in contrast to the evolution of human tools there is little sign that chimpanzees have diversified tool designs through cumulative changes (Dean et al. 2012). Hunt and Gray (2003) speculated that cumulative changes to relatively simple wide tool manufacture led to more effective pointed tools in the form of the narrow tool and stepped tool designs. Although the co-occurrence of distinct pandanus tool designs in space and time that vary in manufacture complexity is consistent with design diversification, independent invention of each design remains a possibility (Lewis and Laland 2012). While a lack of recapitulation of manufacture techniques clearly differentiates three distinct pandanus tool designs, this feature in rudimentary tools might also be associated with independent invention. Here, I describe the manufacture and use of a novel pandanus tool design from Parc Rivière Bleue that is an oversized version of the narrow tool design. This finding strengthens the possibility that diversification of NC crows' pandanus tool designs has occurred.

OBSERVATIONS

In March 2005, I collected sections of missing leaf edge from *Pandanus* spp. trees in the Parc Provincial de la Rivière Bleue situated in the Southern Province of mainland Grande Terre, New Caledonia. From evidence of cuts, two of these sections (RB19 and RB89) indicated successful narrow tool manufacture as described above (Fig. 3A, B). The counterparts were on trees ca. 300 m apart on either side of the Gué de la Pourina crossing of the Rivière Bleue (approximate location of trees 22° 6′ S, 166° 40′ E). The two counterparts were in good condition with little sign of decay, indicating that tool removal had occurred in the recent past rather than years ago. They averaged 43.9 cm long and the tools that were removed from them had a minimum width of 5 mm. One of the two counterparts had the characteristic wisp of fiber at the end where the tool was finally removed from the leaf. Surprisingly, the counterparts were both long and relatively wide compared to most narrow tool

counterparts collected previously on Grande Terre, even those from Parc Rivière Bleue (Hunt and Gray 2003). I also collected five similarly-sized sections of missing leaf edge in the adjacent Mois de Mai Valley in Parc Rivière Bleue in 2005 (22° 7′ S, 166° 40′ E; ca. 2.7 km from where RB19 and RB89 were collected). However, decay on the cut edges of these sections meant that I could not be entirely confident that they were associated with successful tool manufacture. I also collected many counterparts along the Rivière Bleue in 2000 (south side) and 2001 (north side), but there were no potential oversized tool counterparts among them.

On 20 March during my visit to Parc Rivière Bleue, I also collected a pandanus tool after it was made and used by an NC crow that closely matched the shapes of the oversized tools that were removed from the two counterparts in Fig. 2. While in a hide watching a feeding table at the Gué de la Pourina crossing (22° 6′ S, 166° 40′ E), I observed two NC crows; one was a banded adult and from its independent foraging behavior the other appeared to also be an adult. Later in the crows' visit, I heard the distinctive sound of *Pandanus* sp. leaf being ripped. Soon afterwards I saw the unbanded crow using a long, flexible tool. It was using the tool to probe into the large cylindrical sheath on the end of a dead palm leaf that was caught in living trees ~4 m above the ground. The crow was holding one end of it and moving the tool in an obvious attempt at foraging for food there. I collected this tool, which was a 49.2 cm strip of freshly removed barbed *Pandanus* sp. leaf-edge ranging from 7–13 mm wide (Fig. 3C). To my knowledge, this is the longest tool that an NC crow has been known to make and use when foraging naturally in the wild. I found the counterpart of the tool on a nearby *Pandanus* sp. tree (Fig. 3C). The tree was situated between the two trees from which I had collected counterparts RB19 and RB89. From inspection of the tool and its counterpart, the manufacture of the tool was the same as that described above for a narrow pandanus tool. There was a cut to remove the tool from the leaf at the end of a long rip towards the trunk, which left a definite wisp of fiber. An interesting aspect of the tool's manufacture was that there were two distinct cuts to start the manufacture process at the end distal to the trunk, making it unlikely that the first deepish cut was a misjudged attempt to manufacture a narrow tool.

The mean length to mean minimum width ratio of the three oversized counterparts was 76:1 (457 mm: 6 mm). This same ratio for the 1,022 sections of missing leaf edge described as narrow tool counterparts in Hunt and Gray (2003) was larger at 167:1 (234 mm: 1.4 mm). Forty-seven of these 1,022 sections were longer than 40 cm, but only eight of the 47 had a minimum width >3 mm (GRH, unpubl. data). Thus the three oversized tools described here do not simply reflect a relative enlargement of the narrow tool design, but are instead relatively wider than the narrow design. It should be noted that the 1,022 narrow sections of missing leaf edge were associated with both completed narrow tool removal and ripped strips that were left to decay and drop off leaves.

Narrow tool making was found to commonly occur at six sites on Grande Terre in 2000, including along the Rivière Bleue (Hunt and Gray 2003). All the eight sections above that were longer than 40 cm and had a minimum width >3 mm were collected at Mt Humboldt (21° 53′ S, 166° 26′ E; 33.6 km from where the 3 oversized tools were collected in Parc Rivière Bleue) (mean length = 45.9 cm, SD = 3.79; mean minimum width = 4.8 mm, SD = 0.89; n = 8). Decay on the edges of these eight leaf sections meant that completed tool manufacture could not be verified.

DISCUSSION

I described the manufacture of three oversized tools made out of leaves of *Pandanus* spp. along the Rivière Bleue. Manufacture of these tools was based on the technique used to make the previously described narrow pandanus tools, but they were relatively wider than narrow tools. The counterparts were recent ones within 300 m of each other, so they could have been manufactured by the same NC crow. The presence of similar-shaped missing leaf edge in the nearby Mois de Mai Valley and at Mt Humboldt suggests that NC crows might deliberately make and use these oversized tools outside the Rivière Bleue area.

To recall, the wide tool, narrow tool and stepped tool designs are made using non-recapitulating techniques, where the narrow design is always associated with an initial rip towards the trunk. However, the manufacture of the oversized tools involved the basic actions used to make a narrow tool, except that a long and relatively wide strip is ripped towards the trunk before it is finally cut from the leaf. Although the number of

oversized tools described here is small (n = 3), the data suggest that they represent a novel design. On counterparts A and C (Fig. 3), two cuts were made in from the leaf edge when starting manufacture, making it less likely that the crow(s) meant to rip a narrower strip of leaf edge. Only one cut is used to begin narrow tool manufacture. Furthermore, the direct observation of an NC crow using an oversized tool, and in a functionally appropriate way in a deep probe site, increases the likelihood that the three oversized tools made in the vicinity of the Gué de la Pourina were not incorrectly made narrow tools.

Although our close primate relatives and certain bird species are capable of impressive tool skills (Shumaker et al. 2011), there is no irrefutable evidence that they have cumulatively improved their tools over time (Dean et al. 2012). If a species had evolved this ability it would offer a valuable model to learn about a critical stage in human evolution. I next suggest three reasons why the oversized design increases the possibility that diversification has occurred in NC crows' pandanus tool designs. First, in contrast to the non-recapitulating techniques to make each of the three known pandanus tool designs, the cutting and ripping actions to make both narrow tools and oversized tools are very similar. For rudimentary tool designs, this similarity of manufacture reduces the possibility of independent invention. Second, narrow tool making was common along the Rivière Bleue where the three oversized tools described here were made. Therefore, the NC crow(s) making oversized tools potentially had access to information about narrow tool manufacture as it developed its tool skills as a juvenile. This is because juveniles' pandanus tool development is highly scaffolded by their parents' tool making (Holzhaider et al. 2011). Narrow tools are also made in the Mois de Mai Valley and at Mt Humboldt where oversized-like tools are also possibly made (Hunt and Gray 2003; GRH, pers. obs.).

Third, all three previously described pandanus tool designs were found to be made in Parc Rivière Bleue in 2000 (Hunt and Gray 2003), where counterparts of each design can sometimes occur on the same *Pandanus* sp. tree (GRH, pers. obs.). This intriguing situation could mean that the three designs have a very similar function and result from independent invention. Alternatively, it might mean that the designs have a common origin and that each one offers functional advantages across different but overlapping sets of probe sites. These scenarios assume that shape variation in independently invented, highly similar designs in the same habitat is less likely to be closely associated with ecological function when compared to related designs with a single origin (Stout et al. 2010). Therefore, a close relationship between ecological function and shape variation between very similar designs (e.g., NC crows' pandanus tool designs) would be consistent with diversification.

There is qualitative evidence that different pandanus tool designs are associated with different foraging strategies. The oversized tool described here was manipulated in a deep probe site. I have also previously collected two narrow tools that NC crows were using in non-*Pandanus* spp. trees: a 37.8 cm long tool that an NC crow had used to probe into a deep hole in a hollow branch of a living tree in the Mois de Mai Valley (tool 'x' in Hunt 1996), and one an NC crow was using in an unidentified probe site near Mt Ouin in 2000. I have now observed an NC crow at three different locations using either a narrow tool or an oversized tool in non-*Pandanus* spp. trees. The behavior of two of these three crows suggested that narrow tools and oversized tools may be used outside *Pandanus* spp. trees particularly for exploring deep probe sites to disturb and catch prey residing there. My own manipulation attempts showed that the extra width of oversized tools enabled more controlled manipulation in a deep probe site compared to conventional narrow tools. However, narrow tools may be efficient in probe sites such as deep, empty holes where stiffness is not necessary. These tools are also used to probe in the bases of *Pandanus* spp. leaves where a thick layer of detritus commonly occurs (see Fig. 1). I have found narrow tools at several sites left in the central V-like channel of a *Pandanus* sp. leaf and extending into this detritus. When a pandanus tool is inserted into, and guided by, this channel narrowness rather than stiffness might be the crucial functional aspect that provides the best chance of capturing prey. Observations of free-living NC crows show that wide tools appear to be used mainly for foraging in *Pandanus* spp. trees. This is the case on the island of Maré where NC crows are rarely seen to use wide tools outside of *Pandanus* spp. trees (Hunt and Gray 2007). Furthermore, my inspection of *Pandanus* spp. trees for tool activity in Parc Rivière Bleue and on Maré found that wide tools are often left in probe positions at the bases of leaves (Hunt and Gray

2007; GRH, pers. obs.). As with narrow tools, the multi-stepped tool design appears to be more efficient than the wide tool design for probing in a range of different locations. I have observed NC crows at sites often transporting the more complex-shaped stepped tools and using them to probe for prey in a range of forest trees not just *Pandanus* spp. trees. Thus the widely manufactured tapered design appears to be the multi-purpose 'Swiss army knife' of pandanus tool designs, providing a tool that is both stiff and pointed and functionally efficient across diverse probing sites (Hunt and Gray 2003).

Lewis and Laland (2012) dismiss the suggestion of design diversification in NC crows' pandanus tool manufacture because independent invention of each design cannot be ruled out. However, in early human tool making insightful inferences can be made about past behavior by examining both artefacts and contemporary behavior (e.g., Faisal et al. 2010, Stout et al. 2010). Although the artifactual and behavioral data presented here are mostly qualitative, they provide reason to suspect that different probing requirements might explain some of the shape variation in NC crows' pandanus tool designs. If future research confirms this hypothesis, it would further strengthen the case for diversification of pandanus tool designs via cumulative change.

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Courtship and Aggressive Behavior of the Least Grebe in the Breeding Season

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ABSTRACT.—The study investigated behaviors of Least Grebes *Tachybaptus dominicus* during the breeding season. Agonistic postures and interactions and courtship rituals already mentioned by other authors are described in more detail and new pair bonding displays detected, especially Parading in Z posture and the Diving ceremony, are added to our knowledge of the species. The results are discussed in relation to the prevalent phylogenetic hypothesis for the grebe family.
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So far, the published knowledge about the behavior of the Least Grebe *Tachybaptus dominicus* is scant, especially with respect to courtship displays. The only descriptions of pair bonding rituals are by Zimmerman (1957), Palmer (1962) and Storer (1976, 1992). Whereas Zimmerman (1957) described in much detail a single ceremony later termed Rushing by Storer, Palmer (1962) gave but a vague description of the usage of flying and gliding during courtship and mentioned greeting calls between established pairs. He admitted however that there is considerable displaying by the species in spring. Storer (1976, 1992) added much information about agonistic behavior and territory defense of Least Grebes in the breeding season and provided complete descriptions of mounting, reverse mounting, and post-copulatory displays. With respect to water courtship, his account remained rather short and mainly mentioned Advertising and duetting trills once pairs are formed. Storer also included the knowledge already provided by Zimmerman (1957) and Palmer (1962) but admitted that he himself had neither observed the Rushing display nor any display flights.

Behavior is determined to a certain extent by phylogenetic adaptations. Comparisons of closely related species frequently reveal behavioral patterns that point to a common phylogenetic origin (Eibl-Eibesfeldt 1975). Lacking knowledge about the ethology of a species, especially with respect to courtship and aggression, is an obstacle to phylogenetic analyses. It can be lowered by increased knowledge of the species.

During a stay in south Texas in July 2013, I concentrated my observations on the behavior of Least Grebes, with the aim of adding new details to the knowledge about the species. In the following, I mainly describe the water courtship rituals recorded and add a few details concerning aggressive behavior. I briefly compare the behaviors to those of other grebe species in a similar context.

METHODS

Least Grebes were observed at Estero Llano Grande State Park near Weslaco, Texas on 10 and 13 July, at Santa Ana National Wildlife Refuge near Alamo, Texas on 12 July, at Resaca de la Palma State Park near Brownsville, Texas on 14 July and at Sabal Palm Audubon Sanctuary near Brownsville, Texas on 15 and 17 July. Observation times were daily from 0800 to 1600 Central Daylight Time (CDT) daily. Observation distances were between 10–200 m, though the majority of observations were from rather close (distance $\leq$ 20 m). On Grebe Pond of Estero Llano Grande State Park, a single pair of Least Grebes was present. On Cattail Lake 2 of Santa Ana NWR, and on the resaca at the height of Kiskadee Trail at Resaca de la Palma, each time a pair and a single grebe were recorded. Least Grebes were most numerous at Sabal Palm with three pairs inhabiting the part of the resaca in front of the covered hide and another three pairs present along the boardwalk of Oriole Trail. Least Grebes were sexed according to body and bill size, males being generally larger and heavier billed. Pied-billed Grebes *Podilymbus podiceps* were recorded on none of the water bodies occupied by Least Grebes.

All pairs found were followed for at least some time and all occurrences of displays and agonistic behaviors were photographed using an 800 mm lens and a Nikon D-600 camera. Simultaneously, additional details were tape recorded. All observations were evaluated and completely described in

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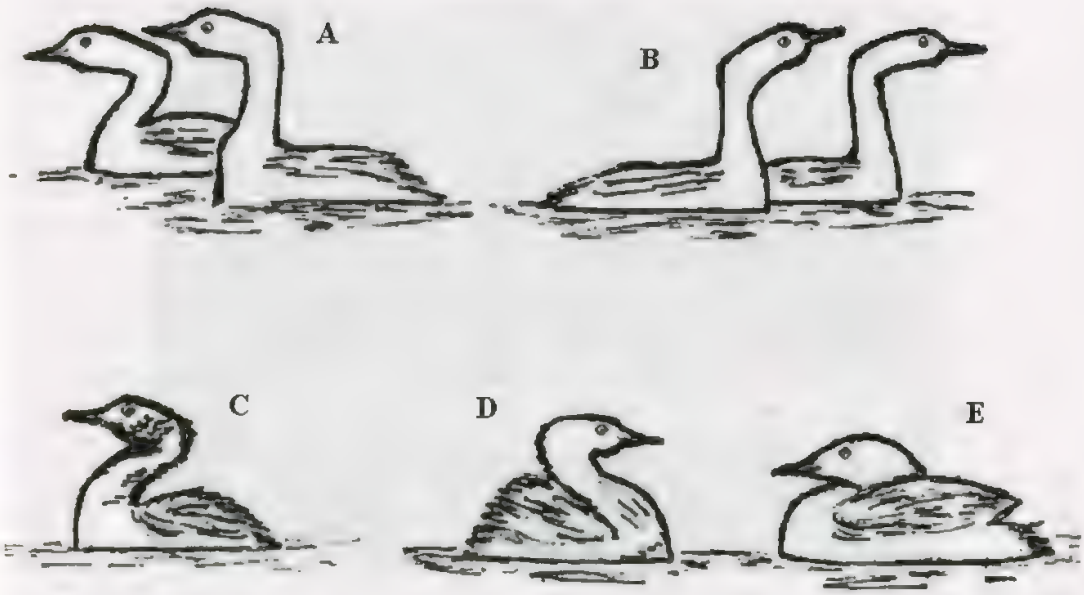

FIG. 1. Postures of Least Grebes: A. Parading in Z posture (swimming), B. Parading in Z posture (slower progress and rotation), C. Z-threat posture, D. Imposing posture, E. gentle Bouncy posture.

the evening of the day when they occurred by combining the voice recordings and the photographs.

RESULTS

Observations of Water Courtship

Most pairs under observation seemed firmly paired in July 2013. It is therefore uncertain if the displays recorded here play a role in the initial phases of pair bond establishment.

Advertising and Response.—Advertising was only observed at Santa Ana. A single female advertised repeatedly trying to attract the attention of a paired male. During advertising, the neck was held about vertical, the bill about horizontal. The rather short crown feathers were raised and the tail was occasionally cocked. Other feathers of the head and neck were relaxed, neither depressed, nor extremely raised.

The paired male suddenly showed up in front of the vegetation. It adopted a particular posture, here termed Imposing posture, with the lower neck leaning obliquely backward. The head was kinked forward to above the lower foreneck and it was held in a horizontal plane. Facial feathers were sleeked while hind neck feathers were raised. The upper head appeared completely flattened. The body was horizontal on the water surface. The mantle feathers were lifted giving the body a fluffy appearance (Fig. 1D). In this posture, the grebe turned its head from side to side, the body rotating simultaneously to a lesser degree. Both grebes then slowly approached one another in this posture. At close range, they started to turn on the water surface and to change their posture for a Z posture as described below under Parading. Unfortunately, the action did not progress further; the regular mate of the male appeared out of the vegetation and chased the odd female. The latter showed little resistance and immediately fled, whereupon the regular female engaged in duet trilling with the male.

Duet Trilling (observed repeatedly in eight pairs).—In the typical duet trilling posture, Least Grebes kept their necks retracted and the lowered head was slightly advanced (Hunched posture). Their wings were slightly lifted over the back. The display could start while both partners were together or after a separation when both joined again. In the latter case, one grebe could cover the distance between them by either swimming or diving. Upon coming together, both partners, still in the Hunched posture, uttered trilling calls while facing. These were continued while the grebes turned on the water surface. There seemed to be no predefined sense for the rotation and the partners could change their relative position on the water surface to one another at random, sometimes facing more or less in the same direction, at others facing in opposite directions.

FIG. 2. Pair of Least Grebes Parading in Z posture at Santa Ana National Wildlife Refuge, Texas.

While turning, both could also drift a bit apart. The pair could also briefly mill around while continuing its calling. Duet trilling as a display could be repeated. It was observed at all locations and occurred likewise in pairs with and without a platform. It always followed agonistic interactions with neighboring pairs as part of the Triumph ceremony.

Parading in Z Posture.—In this display, both grebes swam together in one direction in a posture in which their head, neck and body formed a kind of open Z form. The breast was pushed out and during more rapid progress, it was slightly elevated. Then, some white belly feathers could show up while the body was sloping. In no observation, the breast elevation was however comparable to the drawing of Rushing in Zimmerman (1957). Also, the neck was slightly bent back from the vertical forming a sharp angle at the height of the upper breast. It was again bent forward in its upper part and the head was advanced in prolongation of the kinked part of the neck. The throat was puffed out and the bill was pointing horizontally or even slightly upward (Fig. 1A). The abrupt kinking of the upper neck into the plane of the protruding head made the latter look elongate. In all observations of the display, one partner held its head higher while its mate was generally slightly leading. The progress was not necessarily in a straight line and the pair could occasionally change the direction, especially during slower progress. When coming to a stop, the grebes maintained the posture briefly and appeared to slightly turn their heads from one side to the other before relaxing and engaging in comfort behavior. Performances of the display were observed twice at Santa Ana and Resaca de la Palma, always by the same pairs, and seven times at Sabal Palm by four different pairs.

A pair at Santa Ana was once observed to enter the vegetation in this posture, one mate following the other. This time, both held their heads equally high, their upper neck bent more sharply and their breasts slightly elevated, too (Fig. 1B, Fig. 2). Slowly circling around stands of weeds, the pair seemed to inspect the place, stopping here and there and slightly lifting or lowering the head. Occasionally both grebes rotated either to facing or to facing in different directions. The rotations were rather slow and the grebes maintained a stiff posture. When again coming to face in the same direction, both slowly moved in one direction before the ritual ended.

Parallel Swimming.—Parallel swimming was observed to follow duet trilling or to arise in situations where both partners were moving about together uttering continued calls. Generally, one bird took the lead. In most observations of the three pairs showing the display, this was the female. If parallel swimming arose out of duet trilling, initially the grebes kept a posture with the neck retracted and the plumage of the back raised.

After having been more or less parallel for a few meters, they could stop before resuming the swimming with their heads elevated and their necks slightly bent forward from the vertical. They thus rapidly swam continuously into one direction, most of the time one grebe leading. The swimming speed was variable. In most cases, cackling calls were uttered by the progressing grebes. These halted after having covered some distance. They remained briefly motionless, either slightly leaning their neck back and advancing the head, thus head neck and body forming a kind of not very pronounced Z form with the bill slightly pointing down, or looking around with their heads still high. They could then anew engage in duet trilling with their necks retracted, or one or both birds could dive or engage in preening. To what extent this preening, if performed by both birds, was ritualized is difficult to say as it closely resembled comfort preening. Parallel swimming was observed repeatedly in about all pairs recorded at Estero Llano Grande, Santa Ana, Sabal Palm and Resaca de la Palma.

Diving Ceremony.—This ceremony was only observed once at Resaca de la Palma. The postures adopted during it and the progress of the action appeared however stereotype, ritualized, and showed great similarities with displays involving diving in other grebe species. The ceremony followed Parallel swimming after which the partners had drifted a bit apart. One grebe suddenly uttered a short call and adopted a kind of gentle Bouncy posture (Fig. 1E). This differed from the bouncing initially described for Horned Grebes (*Podiceps auritus*; Storer 1969, Fjeldså 1973) in that the body remained in the horizontal plane and resembled to some extent the Swan posture of the Red-necked Grebe (*Podiceps grisegena*) in the Discovery ceremony. The Least Grebe had its neck folded and its head resting in between the shoulders on the lower neck with the bill slightly pointing down. The wings were slightly lifted and not spread, and the tail was cocked. The second grebe at ~10 m distance about immediately turned to facing in a similar posture and quickly dived. While progressing below the water surface, its mate slowly rotated above for 180° without changing its posture. Now facing in the opposite direction, it could observe the surfacing of its partner at a distance of nearly 10 m. Hardly fully emerged, the grebe had again turned to facing in a posture similar to the one adopted by its mate. Both then put their heads forward and started duet trilling while moving together. Upon joining, they rotated on the water surface. They halted when about facing in opposite directions, but continued their calling. Then they again swam together and briefly milled around before the action stopped.

Weed Display and Ceremonial Building.—Both partners of a pair owning two basic platforms located at some 20 m apart were repeatedly seen picking up single tree leaves from the water surface. They then milled around rapidly, with their necks retracted, their heads advanced and their back feathers and wings slightly lifted, keeping a leaf in the beak and uttering cackling calls. Often one grebe closely followed its mate, sometimes they came a bit apart from one another. Initially, their milling could have no precise direction, and it occurred that they deposited the leaf on the open water surface, one or the other partner again picking it up again before depositing it anew on the water surface (Weed display). In most observations, both grebes at the end approached one platform and deposited their leaves on top, at times immediately lifting them a second time before depositing them anew. It also happened that the leaf deposited by one mate was picked up by the partner only to replace it again on the platform (Ceremonial building). After depositing, the grebes briefly halted in their movements, staring at the platform, before resuming with quite differing activities including preening, real platform building and jumping on top of the platform. The display was only observed with two different pairs at Sabal Palm, ten times in the first and twice in the second.

Rushing.—Rushing exactly as described by Zimmerman (1957) was not observed. Instead a comparable display occurred that was termed Parading in Z posture. In Zimmerman's drawing, the breasts of both grebes were elevated to an extent that even part of the upper belly was above the water surface whereas the tails were submerged. Their upright necks were slightly bent forward, their heads were advanced and slightly above a horizontal plane.

Aerial Display.—No observations corresponded to aerial displays as mentioned by Palmer (1962).

Platform Courtship

A single observation of mounting at Sabal Palm preceded by repeated soliciting confirmed the behaviors as reported by Storer (1976) with respect to inviting by platform bird, pre-mounting

FIG. 3. Two grebes in Z-threat posture rotating on the water surface, Sabal Palm Audubon Sanctuary, Texas.

activities of water bird, mounting, head raising and turning during copulation, dismounting and post-copulatory displays of partners.

Aggressive Behavior

Threat Postures.—The most intense threat posture observed was with two opponents facing, the neck retracted, the head lowered and slightly advanced. The wings were lifted and slightly pushed forward forming a kind of shield behind the head (over 20 observations in five times two different opponents). The posture was observed with head plumage either sleeked or completely raised. Facing opponents could shout at each other and occasionally slowly turn their head in the posture, especially if the threatening lasted.

In total, the Z-threat-posture (Fig. 1C) as described by Storer (1976) was observed at six occasions involving three times different opponents. This posture differs from the Z posture in parading in the raising of back feathers and in the degree of backward kinking of the neck which makes the breast protruding. In no case the threatening grebes looked as gentle as in Storer's drawing. Also, the bending of neck and head was more pointed and looked more exaggerated. Head, neck, and facial feathers were raised giving to head and neck a swollen appearance. The feathers of the crown were sleeked and the upper head appeared flattened. The breast was always pushed out and the body was at times sloping. Mantle feathers were slightly raised. The posturing was quite close to the Imposing posture described earlier. While threatening in this posture, the grebes rotated on the water surface, at times turning their back at the opponent (Fig. 3). In addition, they slowly turned their heads from one side to the other. They almost never directly faced, but rather observed the conspecific out of the corner of their eyes. It occurred that the posturing was interrupted by a brief body or wing shake before being resumed.

The more extreme Bouncy posture adopted during aggression and described by Storer (1976) was only observed once at Sabal Palm. It followed intense fighting ending with a retreat of one opponent. It was the latter grebe that adopted the Bouncy posture with the breast highly elevated and the tail nearly sunken below water, the neck extremely bent backward and folded in the middle and the chin resting on the lower foreneck. It followed threatening in Z-posture by the opponent during which this one slowly advanced. When at close range, one grebe headed forward with flapping wings out of the Bouncy posture. Its neck was jerked forward with the head kinked so as trying to crash into the others breast. The opponent jumped high, simultaneously lowering its head to shield the body. As a consequence, the attack was too low for a hit, but it started an intense fight.

During threatening at close range before starting or in interruption of a kicking combat,

Least Grebes could remain lower on the water with the tail submerged. While screaming at each other with slightly opened wings, they held their neck in S-form rather than in Z-form. Facial feathers and those of the crown were depressed, those of the region of the ear tufts and of the neck raised.

Fighting.—During breast-to-breast combat at the border of a territory, Least Grebes were not only seen kicking with their feet, but they also tried to grasp their opponents with the beak. On one occasion, a grebe got hold of its opponent's wing whereupon the latter beat it and dived with much splashing, followed by the other. When both emerged again, one grebe was behind the other and held the opponent by the neck. Both almost immediately disappeared again under water and this time surfaced a bit apart, one pursuing the other, running with paddling feet and gliding with flapping wings over the water surface.

During fight interruptions, partners could join for duet trilling before opponents returned to threatening.

Whereas mostly males engaged in combat (four observations with two different opponents), on one occasion, a simultaneous fight between males and females was observed. The situation started with both males threatening at close range on the border of their territories. Only one female parading in the Z-threat-posture in the back of its partner was present. The second female was incubating about 50 m away. I had not noticed the latter gliding into the water and diving into the direction of the three others. It suddenly emerged in front of the opponent female and immediately attacked, the males jumping at each other at about the same time. The females' fight was short as one of them, taken by surprise, fled after a short vigorous contact.

Pursuing and Chasing (over 20 observations in at least 10 different grebes).—Fleeing grebes were always pursued over a short distance with feigned attacks, the pursuer now and then leaping forward with extended neck and flapping wings as in an assault, but immediately falling back onto the water surface. Chased grebes either dived or fled with flapping wings over the water surface.

Triumph Ceremony (six observations, twice in different pairs).—Aggressive interactions at territory borders always ended with the opponents adopting a Z-threat posture and slowly drifting apart before relaxing and showing duet trilling with their partners. On three occasions, both partners of a pair were observed in parading and turning on the water surface in the Z-threat posture before joining for duet trilling. This duet trilling differed from duet trilling during greeting in that the pair turned more often in the direction of the neighbors and then held their heads slightly higher with the neck sharply kinked forward just above shoulder height.

DISCUSSION

The present notes are based on few observations and therefore may neither cover the full range of courtship and aggressive behaviors of Least Grebes, nor the variability that probably occurs in the displays described. They correspond however well to Fjeldså's observations from Colombia in 1981 (pers. comm.) that were only very briefly described in his 2004 publication. Faced with the scarcity of precise descriptions in ornithological literature limited to Gross (1949), Zimmerman (1957), Palmer (1962), Storer (1976, 1992) and Patrikeev (2009), they constitute a valuable contribution to our knowledge by adding new displays and providing more detailed accounts. This is important for our correct interpretation and understanding of relationships in this bird family, as outlined by Fjeldså (2004). The results do not challenge the present placement of the Least Grebe in the genus *Tachybaptus*, but provide additional arguments for its correctness. Based on Bandorf (1970) and on my own regular observations of European Little Grebes (*T. ruficollis*), duet trilling, perhaps best termed Trilling display to separate the vocalization from the ritual, and related displays in both *Tachybaptus* species are very similar with respect to performance and contexts of occurrence. A comparable duet trilling is mostly absent from *Podiceps* species. The Trilling ceremony of *P. auritus* with a notably developed vocalization in Western Palearctic populations (Fjeldså 1973) may come rather close. Also the Hunched display of Black-necked (*Podiceps nigricollis nigricollis*) and Eared grebes (*P. n. californicus*) is not that different. It however generally lacks a subsequent milling around (Konter 2012). As a display, duet trilling as performed by *Tachybaptus* species resembles most the Triumph ceremony of Pied-billed Grebes. After separation or after aggressive encounters, partners in this species meet in a Hunched posture and mill around each other (Muller and Storer 1999).

The single observation of a response to Advertising is insufficient for a comparison with other grebe species. It does anyway not help for detecting similarities with Little Grebes as little is known about how pair formation progresses in that species (Bandorf 1970).

In many grebe species, forms of Parading are present in courtship and Triumph ceremonies. During courtship, they are generally performed in postures that differ from the Z-posture of Least Grebes. I do not know of a comparable ritual in Little Grebes. The posture of Pied-billed Grebes in their Circle display may be closest, although the display is used by opponents at territory borders in which the rotations are not necessarily synchronized (Muller and Storer 1999). In this sense, Circling display of Pied-billed Grebes and threat-parading in Z-threat posture could be corresponding. As courtship rituals, Parading in Z-Posture in Least Grebe and the Pirouette Ceremony of Pied-billed Grebes (Fjeldså 2004) may have evolved out of the agonistic behaviors. A comparable parading is also present in Hoary-headed Grebes (*Poliocephalus poliocephalus*; Fjeldså 1983).

Zimmerman's (1957) Rushing display was neither observed by Storer (1976) nor during this study and one may question to what extent it differs from either Parallel swimming or Parading in Z-posture as Zimmerman's drawing looks like a combination of both.

The new-described Diving ceremony appears like a simple precursor of the Discovery ceremony occurring in *Podiceps* species. It differs however in the posturing of the passive bird that does not fully expand its wings as in *Podiceps* species like Great Crested (*P. cristatus*; Simmons 1975) or Eared grebes (Cullen et al. 1999, Konter 2012). It neither matches the less spectacular Swan posture with raising and little lateral opening of the wings in Red-necked Grebes (Wobus 1964). A similar Bouncy posture as shown here by Least Grebes is used by Little Grebes in agonistic behavior (Bandorf 1970, AK pers. obs.). The surfacing of the diving Least Grebe is in a more basic posture that is not comparable to the upright posturing with water treading in *Podiceps*. Generally, the Least Grebe's ceremony appears more primitive and may have been a precursor of the more evolved Discovery ceremony. *Poliocephalus* spp. show a similarly simple diving ceremony, the diving bird going beyond the other to surface behind it (Fjeldså 2004). I have so far not observed a similar display in Little Grebes. Except when preceding the Trilling display, Little Grebes only appear to use diving during their Rocket display (Konter 2010) in which the diving bird however surfaces directly in front of the waiting partner, showing head jerking and anew diving, but no duet trilling.

Storer (1976) concluded that the Least Grebe is possibly best placed in the *Tachybaptus* subgroup, but he also suggested that the long isolation from its Old World relatives could have evolved differences warranting a separate subgenus. Based on morphological characters, Fjeldså (2004), in his revised phylogeny of the grebes, proposed a change to the topology of the *Tachybaptus* branch. The three most distinctive species—Australasian (*T. novaehollandiae*), Madagascar (*T. pelzelnii*) and Least grebes formed one branch that was sister to the widespread *ruficollis/rufolavatus* groups. Besides similarities, my observations also detected differences in the courtship of American Least and Eurasian Little grebes, especially in the newly described rituals of Parading and in the Diving ceremony. Further progress to achieve a complete inventory of pair bonding displays in all *Tachybaptus* species is however needed before a comparison of their pair bonding and agonistic behaviors can lead to a valuable contribution in a phylogenetic context.

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Video Evidence of Infanticide by a Female Red-winged Blackbird

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ABSTRACT.—Several hypotheses have been proposed to explain infanticide in animals, but the behavior has only been observed in a few bird species. I describe video evidence of infanticide by a female Red-winged Blackbird (*Agelaius phoeniceus*) at a nest in Valley Forge National Historical Park in Pennsylvania. A female Red-winged Blackbird was seen pecking and pulling at the sole remaining 5-day-old nestling and eventually pulled the nestling from the nest until it fell to the ground. A female Red-winged Blackbird later returned to the nest with food 1 hour after the infanticide and made several visits with food in its bill. The last visit to the empty nest occurred 7 hours after the infanticide occurred. There were not sufficient plumage differences between the feeding and attacking bird to determine conclusively that they were different birds. The occurrence of infanticide could be explained by several hypotheses and might be more common in Red-winged Blackbirds than has been reported. For example, infanticide in Red-winged Blackbirds could increase male parental investment as is seen in other polygynous species. Misplaced aggressive behavior under stressful conditions; however, is also a possible explanation for this single case of infanticide. *Received 23 August 2013. Accepted 18 October 2013.*

Key words: female-female competition, infanticide, nest, nestling, parental care, polygyny, video.

Several hypotheses have been proposed and tested to explain infanticidal behavior. Four hypotheses frame nonparental infanticide as an adaptive behavior (Hrdy 1979): (1) killing young of another parent will increase the likelihood of mating with this individual or decrease the time until mating (sexual selection hypothesis), (2) infanticide will reduce competition for resources such as nest sites or food (resource competition hypothesis), (3) infanticide will direct more parental investment from a polyandrous or polygamous mate toward the offspring of the perpetrator (parental investment hypothesis), and (4) direct exploitation of the young as food (cannibalism hypothesis). The parental investment hypothesis often is considered a special case of sexual selection infanticide, but I discuss it as a separate hypothesis to illustrate better the situations in which infanticide might be an adaptive behavior. A nonadaptive hypothesis for infanticide proposes that instances of killing young occur as a result of social pathology in response to stressful situations, for example, overcrowding (pathology hypothesis) (Hrdry 1979). In addition, infanticide by a parent might be adaptive by killing weaker or sick young to allow for greater resource allocation to other offspring thereby increasing the survival or future reproductive success of the remaining young (brood reduction hypothesis) (Mock 1984).

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The pathology hypothesis is generally refuted because it cannot explain why infanticide is observed regularly in some taxa even with low densities and little human disturbance (e.g., primates; Hiraiwa-Hasegawa 1988). Rare occurrences of infanticide, however, might be caused by misdirected aggressive behavior in extreme circumstances (Hrdy 1979). The cannibalism hypothesis is not well supported outside of gulls and skuas because usually the victims are not eaten by the attacker (Mock 1984). Brood reduction often explains parental infanticide and has been reported in several bird species (e.g., Urrutia and Drummond 1990, Klosowski et al. 2002). Nonparental infanticide in birds often is explained by the sexual selection, resource competition, and parental investment hypotheses.

Sexual-selection driven infanticide has been demonstrated in several species of birds. Both male and female House Sparrows (*Passer domesticus*) have been observed committing infanticide to increase mating opportunities in a polygynous population (Veiga 1990a, 2004). Infanticide by females of two polyandrous species that demonstrate behavioral sex role reversal (male care for eggs and young), Wattled Jacana (*Jacana jacana*) and Northern Jacana (*Jacana spinosa*), also supports the sexual selection hypothesis (Stephens 1982, Emlen et al. 1989). Stacey and Edwards (1983) also reported suspected infanticide by an immigrant female in a breeding group of Acorn Woodpeckers (*Melanerpes formicivorus*), which shared a communal nest; the immigrant female subsequently laid eggs in a different nest cavity. Female Tree Swallows (*Tachycineta bicolor*) also committed infanticide when replacing missing females at a nest (Chek and Robertson 1991). Infanticide was also observed by replacement male and female House Wrens (*Troglodytes aedon*) in Panama (Freed 1986).

The resource competition hypothesis is supported by evidence of infanticide at nests of widowed female Tree Swallows by males that subsequently breed in the nest, a limited resource, either with the widowed female or another female (Robertson and Stutchbury 1988). Lee et al. (2011) also hypothesized that infanticide by a Black-billed Magpie (*Pica pica*) in Korea was driven by potential expansion of the breeding territory by the individual that was killing nestlings.

Infanticide by females to increase parental investment by males has been reported in House Sparrows (Veiga 1990b) and Great Reed Warblers (*Acrocephalus arundinaceus*) (Bensch and Hasselquist 1994, Hansson et al. 1997). The feeding rate by males was lower at nests of secondary females when compared with the primary female for both House Sparrows and Great Reed Warblers (Veiga 1990b, Bensch and Hasselquist 1994). Secondary Great Reed Warbler females received more male assistance and fledged more young when the primary female's nest failed (Bensch and Hasselquist 1994, Bensch 1996). Experimental evidence of destruction of primary females' eggs by secondary females in Great Reed Warblers (Hansson et al. 1997, Trnka et al. 2010) supports the idea of infanticide by secondary females to secure more parental investment.

Evidence of infanticide has been reported for a limited number of bird species, but infanticide might be misclassified as predation if infanticide is not observed directly. Here, I describe video evidence of the first reported occurrence of infanticide by an icterid, a female Red-winged Blackbird (*Agelaius phoeniceus*), and discuss potential hypotheses for infanticide within the species.

OBSERVATIONS

Red-winged Blackbirds are common in meadows at Valley Forge National Historical Park in Pennsylvania. Blackbirds occurred at 86% of survey points in meadows and the estimated density was 6.33 birds per ha in 2011 and 2012 (LDM, unpubl. data). Nests of Red-winged Blackbirds were located as part of a larger study of the nesting ecology of birds in grasslands at Valley Forge.

A nest of Red-winged Blackbirds with two 2-day old nestlings was found on 5 June 2012 in a meadow at Valley Forge National Historical Park in Pennsylvania. The nest was 25 cm above ground in an area dominated by fescue grass (*Festuca* spp.). The nesting area was about 300 m from a small area (<1 ha) dominated by broadleaf cattails (*Typha latifolia*) with a high density of breeding Red-winged Blackbirds. Another nest of Red-winged Blackbirds was located 62 m northwest of the described nest; it was active at the time of the infanticide and fledged at least two young on 14 June.

On 8 June, a student researcher and I returned to the nest to install a video camera to monitor the nest. Upon arrival at the nest at about 0630 EST, I observed two 5-day old apparently healthy nestlings in the nest. We moved 15 m from the nest to install the digital video recorder (DVR). Upon return to the nest about 10 mins later, one dead nestling was on the ground near the nest;

no obvious signs of injury or predation were observed during a cursory examination of the nestling. A miniature weather-proof infrared digital video camera was placed 10 cm from the nest and connected to the DVR at 0646.

On 11 June, the nest was found empty and intact. Review of the video showed activity at the nest within minutes of camera placement by a female feeding the nestling at 0650. A female made eight feeding trips, removed two fecal sacs, and brooded the nestling between 0650 and 0802. A female Red-winged Blackbird came to the nest without food at 0804. The female blocked the camera's view of the nestling, but appeared to peck and pull at the nestling for 4 mins (Supplemental Material A). A female returned to the nest at 0809 and pulled the nestling to the rim of the nest and tore and ate tissue from the nestling. The young appeared still alive when the female left at 0810. A female pulled the nestling causing it to fall to the ground at 0811 (Supplemental Material A). It is likely the nestling found on the ground during camera installation on 8 June also was removed by the same female, but this was not video recorded.

A female returned to the nest 36 secs after the nestling fell. A female was present at the nest for most of the next hour. At 0911, a female brought food and spent 6 mins at the nest before eating the food item (Supplemental Material B). A female visited the nest regularly for the next 4 hrs and 20 mins including four trips with food. The last visit with food occurred at 1455, 6 hrs and 44 mins after the infanticide (Supplemental Material C). A female returned to the nest at 1508 without food and departed at 1510. No further activity was seen at the nest before the camera was removed on 11 June.

To rule out the possibility of parental infanticide, I reviewed the video for differences in plumage or feather wear to confirm the presence of two different females. No obvious plumage differences were detected between the feeding and attacking birds. Slight variations in the shape of the white eye stripe and the shape and wear of rectrices were observed, but differences in positions of the bird(s) and lighting prevented a definitive conclusion.

DISCUSSION

This is the first published report of infanticide by a Red-winged Blackbird, but removal of nestlings from a nest by a female Red-winged Blackbird and suspected infanticide by a female after a disturbance at the nest have been observed (K. Yasukawa, pers. comm.). This single occurrence of infanticide does not provide enough evidence to determine the ultimate cause of the behavior or whether the behavior was adaptive. Despite the inability to distinguish between two different females, there is little support for parental infanticide because the only remaining nestling was killed, thus refuting the brood reduction hypothesis as an explanation. In addition, the frequent feeding visits up to 7 hrs after the event suggest there were likely two different females at the nest. The pathology hypothesis, however, cannot be rejected because this is a single instance of infanticide that might have resulted from aberrant behavior caused by stress from the presence of researchers or another environmental cue. The observation of consumption of tissues from the nestling supports the cannibalism hypothesis, but does not rule out the other hypotheses as the ultimate drivers of infanticide.

Female infanticide in Red-winged Blackbirds is not consistent with the sexual selection hypothesis given the high degree of polygyny in the species (Searcy and Yasukawa 1995). The large harem size of males demonstrates that females are able to obtain a mating opportunity in the presence of other females. In addition, Searcy (1988) demonstrated that resident females do not negatively affect settlement by other females, although Hurly and Robertson (1984) found it took new females up to a week to begin nesting. Therefore infanticide would not increase the likelihood of obtaining a mating opportunity and the sexual selection hypothesis would not be consistent for explaining infanticide in Red-winged Blackbirds.

The resource competition hypothesis is consistent with what is known about female interactions among Red-winged Blackbirds. Aggression is common among females within a harem with females repelling intruding females from their nesting area (Nero and Emlen 1951, Hurly and Robertson 1984). Yasukawa and Searcy (1981) also concluded that female behavior indicated a competitive relationship in regards to other females in a harem. In addition, females tended to win more aggressive interactions and have greater access to supplemental food near her nest (Roberts and Searcy 1988). Thus an infanticidal female might have greater access to resources if she is more likely to win aggressive encounters against a female that does not have an active nest. The relatively high density of breeding Red-winged Blackbirds at Valley Forge is consistent with the possibility of infanticide as a result of competition for resources.

Differential male investment among nests within a territory described in previous studies support the parental investment hypothesis for explaining infanticide in Red-winged Blackbirds. Yasukawa and Searcy (1982) suggested that aggression among females was a strategy to increase male parental investment toward their offspring. The percentage of males providing parental assistance in feeding nestlings ranged from 29–88% in midwestern and eastern populations (Searcy and Yasukawa 1995). Males that did provision nestlings, however, did not do so equally; nests of primary and secondary females were likely to receive more male parental care than tertiary nests and beyond (Muldal et al. 1986, Yasukawa et al. 1990). Additionally, nests with older young were fed more than nests with younger nestlings (Yasukawa et al. 1990). Nests with male assistance fledged more young than nests without help (Muldal et al. 1986, Yasukawa et al. 1990, Patterson 1991). A female that commits infanticide at a nest initiated earlier or belonging to a more dominant female might obtain more male assistance and increase her reproductive success. The close proximity of an active nest of Red-winged Blackbirds is consistent with the possibility of infanticide to secure male assistance.

A definitive conclusion of the ultimate cause of infanticide in Red-winged Blackbirds, if it is more widespread, cannot be ascertained from a single event. I provide rationale supporting several hypotheses based on a single event and what is known of the breeding ecology of Red-winged Blackbirds, but these hypotheses need not be mutually exclusive. The evidence supporting the parental investment hypothesis for Great Reed Warblers and House Sparrows along with reduced male parental care for less dominant females in a harem, however, suggests that infanticide by Red-winged Blackbirds might result from competition for male assistance among females and might be expected to be more common than has been reported. Red-winged Blackbirds, however, have been studied extensively and few instances of infanticide have been observed, suggesting my observation might be an isolated incidence of pathological infanticide (Searcy and Yasukawa 1995). Another case of suspected infanticide by a female Red-winged Blackbird also occurred following a disturbance at the nest (K. Yasukawa, pers. comm.), suggesting disturbance at the nest might increase the likelihood of a female killing young. Monitoring of nests using video cameras could provide more information on the rate of infanticide within populations of Red-winged Blackbirds.

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Breeding Records of Black-capped Vireo (*Vireo atricapilla*) in Northeastern Mexico

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ABSTRACT.—We conducted field work during May–July 2005 in the Mexican states of Nuevo León, Tamaulipas and San Luis Potosí. We observed breeding activity of Black-capped Vireos and found active nests in northwestern Nuevo León and southwestern Tamaulipas. These findings represent the first documented nests for those states, and for the latter state, the first records of Black-capped Vireos nesting below the Tropic of Cancer. Our findings suggest that the breeding range of Black-capped Vireos should be extended approximately 520 km to the southeast of the previous known nesting area near Ocampo, Coahuila. *Received 25 June 2013. Accepted 6 September 2013.*

Key words: Black-capped Vireo, breeding, Mexico, nests.

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The Black-capped Vireo (*Vireo atricapilla*) is classified as a vulnerable species internationally (BirdLife International 2013), and as Endangered by the U.S. Fish and Wildlife Service (Ratzlaff 1987), Texas Parks and Wildlife (TPWD 1988), and Secretaría Medio Ambiente y Recursos Naturales (SEMARNAT 2010). Threats considered to be of greatest conservation concern are brood parasitism by Brown-headed Cowbirds (*Molothrus ater*), and habitat conversion and destruction (USFWS 1991, Wilkins et al. 2006). The historical breeding range for this species extended from Kansas to northwestern Mexico (Coahuila, Nuevo León, and Tamaulipas; USFWS 1991, Howell and Webb 1995). Currently, the breeding range includes portions of southwestern Oklahoma, central Texas, and northern Coahuila (Grzybowski 1995). Although authors such as Graber (1961), Marshall et al. (1985) and Benson and Benson (1990) mentioned potential reproductive

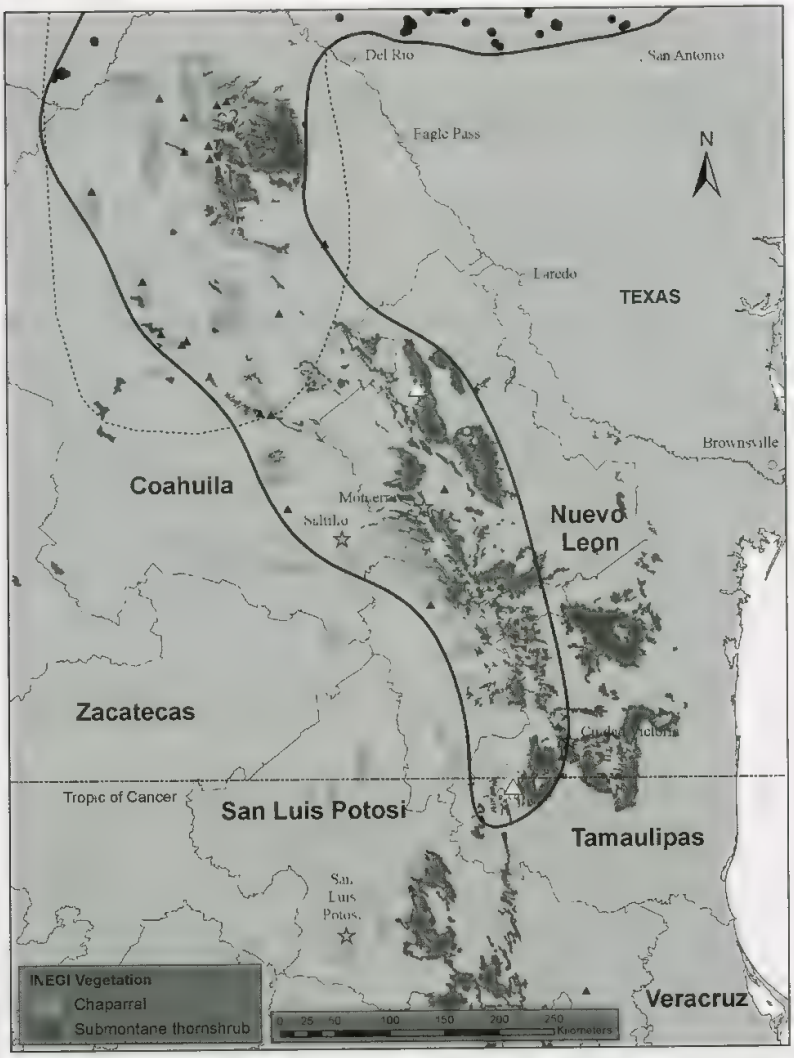

FIG. 1. Proposed (dark line) and historic (dotted line) boundaries for breeding range of Black-capped Vireos in Mexico. Black dots indicate where Black-capped Vireos were observed in Texas (Texas Natural Diversity Database 2008), previous studies in Mexico (black triangles; Graber 1961, Marshall et al. 1985; white circles, Farquhar and Gonzalez 2005) and for nests (white triangles) documented in present study.

habitat in Mexico for Black-capped Vireos, only a few nests have been described. The few nests documented were located in two small mountain chains in central Coahuila (n = 5, Sierra Padilla and Sierra Masera; Graber 1961), and in northern Coahuila (n = 4, Rancho La Escondida; Farquhar et al. 2003). We document here the first records of Black-capped Vireos nesting in Nuevo León and Tamaulipas, which effectively extend their known breeding range southward over 500 km, and into the Tropic of Cancer (Fig. 1). In addition, we present the first published record of brood parasitism by Brown-headed Cowbird (*Molothrus ater*) for this species in Tamaulipas.

In May–July 2005, we visited potential breeding habitat known to have documented sightings of Black-capped Vireos (CCF, unpubl. data) located within chaparral and submontane thornshrub (INEGI 1996) in Nuevo León and Tamaulipas. Our primary objective was to determine presence of Black-capped Vireos and, if located, attempt to determine breeding status, locate nests, and characterize vegetation. As access to suitable habitat is often difficult for various reasons (e.g.,

locating and obtaining permission from landowners, navigability, security), we focused primarily on areas in which access could be regularly obtained in areas with good habitat in north central Nuevo León (a private ranch, Rancho Real de Minas Viejas, near municipality of Bustamante) and southwestern Tamaulipas, on Hwy 101 connecting Palmillas and Bustamante, and along an unnamed road that heads northwestward to Miquihuana from that highway. We visited these areas approximately once per month during the survey period in an effort to visually or aurally document the occurrence of Black-capped Vireos. During those visits, we searched for adult females, noted behavioral cues such as singing males, alarm calling (e.g., "shredding;" Graber 1961), nest material transport by either sex suggestive of nesting activity and presence of fledglings.

In May, we located three nests at Rancho Real de Minas Viejas, Bustamante, Nuevo León. Two nests were found on 16 May, and a third on 17 May. The first of the nests found on 16 May (26° 39′ 05″ N, 100° 22′ 05″ W; 930 m asl) was located 1.1 m above the ground in a 1.7-m evergreen sumac (*Rhus virens*). This nest contained three 5- to 6-day-old Black-capped Vireo nestlings that were tended to by both parents. The second nest we found on 16 May (26° 38′ 59″ N, 100° 22′ 03″ W; 920 m asl) was located 1.4 m from the ground on a 1.8-m tall evergreen sumac. This nest contained two eggs from Black-capped Vireos with the nest guarded by the male parent. The third nest, located 17 May (26° 39′ 05″ N, 100° 22′ 07″ W; 938 m asl), was found 0.8 m above the ground in a 1.4-m tall thickleaf milkberry (*Chiococca pachyphylla*). We observed one egg from a Black-capped Vireo in this nest.

Later in the same season (2005), we found two nests at a site in Tamaulipas. The first nest (23° 21′ 51″ N, 99° 36′ 20″ W; 1,492 m asl) was discovered 12 June, 0.8 m above the ground in a 1.4-m tall lantrisco (*Rhus pachyrrachis*). In this nest we found four 2-day-old Black-capped Vireo nestlings along with one egg from a Brown-headed Cowbird. The second nest (23° 21′ 59″ N, 99° 36′ 12″ W; 1,569 m asl), found 1 July in the same general area, was located 0.8 m above the ground in a 1.5-m tall orchid tree (*Bauhinia ramossisima*). This nest contained an unhatched egg from a Black-capped Vireo, and two recently fledged Black-capped Vireo chicks were seen nearby. Upon return visits between 29 June and 2 July we recorded observations on 20 adults and four fledglings (Farquhar and Gonzalez 2005) to verify that the area supported at least a small breeding population of Black-capped Vireos during that time. It is possible these were not initial, but subsequent nesting attempts. Further work here should uncover those details.

The nests we found were cup-shaped and pensile, built in the forks of branches toward the outer foliage, closely matching the description of other nests built by Black-capped Vireos found throughout Texas, Oklahoma (Grzybowski 1995, Wilkins 2006), and Coahuila (Graber 1961). Our nests were located in typical Mexican submontane thornshrub vegetation, including lantrisco, orchid tree, and thickleaf milkberry, which are new additions to the extensive list of nest substrates previously recorded for Black-capped Vireos (e.g., Grzybowski et al. 1994). For this species, nest substrate varies regionally across the breeding range of Black-capped Vireos (Grzybowski 1995, Wilkins 2006). In Oklahoma, Graber (1961) found many nests located in blackjack oak (*Quercus marilandica*) and post oak (*Q. stellata*); in Texas, they are commonly in Spanish oak (*Q. texana*), Texas persimmon (*Diospyros texana*), evergreen sumac (*R. virens*), and Ashe's juniper (*Juniperus ashei*) (Smith et al. 2012, Pope et al. 2013). In submontane thornshrub habitat in Coahuila, nests previously have been found in low-growing species of oak (*Quercus* spp.) and in madrone (*Arbutus xalapensis*) (Graber 1961).

The shrubs at our nest sites were 1.4–1.8 m tall, within the 2–3 m range reported in the U.S. (Grzybowski et al. 1994, Bailey and Thompson 2007). Nests were located mainly between 0.8–1.4 m above the ground, within the ranges previously reported for the species; no other data are published for this species in Mexico. Many factors are at play in determining nest placement, including herbivory (e.g., by goats and deer), size of trees and shrubs, and predators (Grzybowski 1995, Bailey and Thomspon 2007, Smith et al. 2012). Research on conservation and community-level factors (e.g., brood parasitism and nest success in general) limiting local populations of Black-capped Vireos in Mexico is warranted.

The potential breeding habitat for Black-capped Vireos in Mexico is likely quite extensive (Guerrero 2004, Núñez 2007), and the breeding range there has not been fully defined. However,

observation of the five nests presented here confirms that Black-capped Vireos are known to breed in the states of Nuevo Leon and Tamaulipas. We suggest that the breeding range for Black-capped Vireos in Mexico should be extended southward from the previously known nest sites near Ocampo, Coahuila, to at least 23° 21′ N and 99° 36′ E to include the nesting area we documented in southwestern Tamaulipas, constituting a breeding range extension of approximately 520 km. Such an extension places breeding Black-capped Vireos within the Tropic of Cancer, meaning they now must be considered both a Neotropical and a temperate zone breeder, and because of the extension of latitudinal range across distinct ecozones, local adaptive differences in breeding ecology and productivity may warrant investigating (Stutchbury and Morton 2008). We further believe surveys southward in the state of San Luis Potosi, in suitable chaparral and submontane thornshrub habitat on the western foothills of the Sierra Madre Oriental, could eventually yield positive results. This study also provides previously undocumented record of brood parasitism of Black-capped Vireos by Brown-headed Cowbirds for the state of Tamaulipas, a conservation threat that certainly warrants further investigation. Compounding this threat is the year-round presence of Bronzed Cowbirds (*M. aeneus*) also capable of parasitizing broods of Black-capped Vireos (although as yet undocumented). Finally, we feel our data demonstrate the strong need for expanded research efforts on the ecology of Black-capped Vireos and conservation in México without which evaluation of its U.S. Department of Interior listing status would be inconclusive.

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Observations of Glaucous-winged Gulls Preying on Passerines at a Pacific Northwest Colony

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ABSTRACT.—Breeding within a seabird colony can have positive and negative effects for smaller passerine species. For example, they may profit from the anti-predator behavior of the seabirds as well as from the influx of food and nutrients brought into the community. However, these possible benefits might be offset by seabird predation. For instance, gulls are not only fierce defenders of their colony, but also opportunistic feeders. Here, we report predation of Glaucous-winged Gulls (*Larus glaucescens*) on Sooty Fox Sparrows (*Passerella iliaca fuliginosa*), Song Sparrows (*Melospiza melodia*), and a European Starling (*Sturnus vulgaris*), observed on Mandarte Island, British Columbia, Canada. These observations provide new evidence for dietary supplements of Glaucous-winged Gulls and for a disadvantage of passerine life in a Glaucous-winged Gull colony. *Received 11 May 2013. Accepted 24 September 2013.*

Key words: Mandarte Island, passerines, predation, seabird colony, species association.

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Within a community, different bird species share the same biotope and therefore have the potential to interact, particularly during the breeding season when movements are constrained by the location of nests. Depending on their natural history, such breeding associations may provide benefits and costs to each species (Quinn and Kokorev 2002). Benefits include profiting from heterospecific vigilance signals, as well as from physical displacement of predators by members of another species (Quinn and Ueta 2008). For example, because of their aggressive nest defense behavior (Burger and Gochfeld 1996), colonial gulls reduce predation rates on associated species (Young and Titman 1986, Väänänen 2000). Food provided by nesting seabirds can provide additional benefits. For instance, mockingbirds of the Galápagos eat seabird eggs (Harris 1968). Darwin's finches consume eggshells of gulls (Grant and Grant 1980) and feces of other seabirds (Schluter and Grant 1984). Additionally, nutrients brought in by colonial seabirds may sometimes increase the productivity of plants, in turn providing increased food sources (reviewed in Ellis 2005).

Conversely, smaller species breeding within seabird colonies can suffer increased rates of predation and aggression from larger species (Wheelwright et al. 1997). For example, most gulls are known to be opportunistic feeders

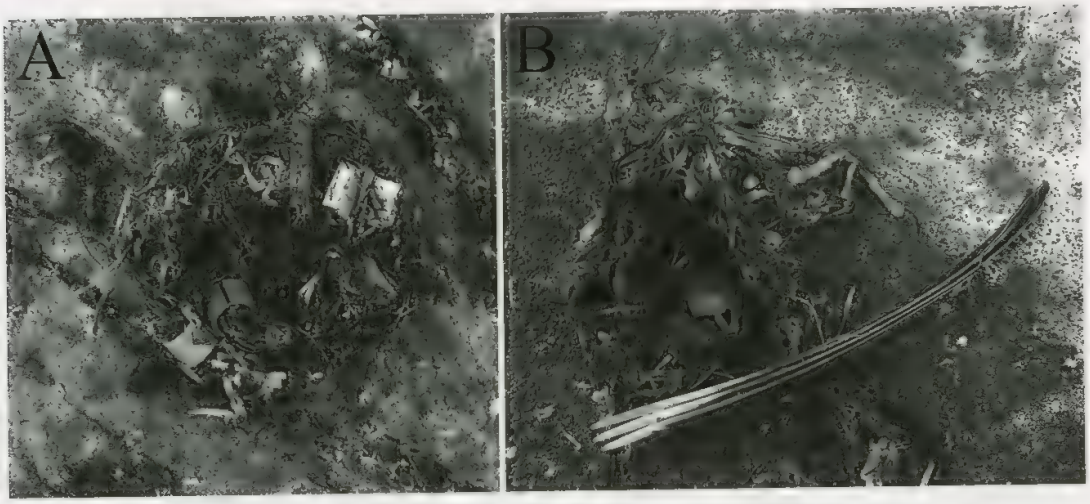

FIG. 1. Photos of gull pellets containing legs and bands (A; found 23 May 2012), and leg and feathers (B; found 29 May 2013), of Sooty Fox Sparrows, found on Mandarte Island, British Columbia, Canada.

consuming a wide variety of foods, including eggs, nestlings, and adult birds of other species (Burger and Gochfeld 1996, Glutz von Blotzheim 1999), potentially increasing the cost of nesting in a gull colony. Although gull predation is often directed at seabirds, several gull species are known to consume adult passerines (reviewed in Glutz von Blotzheim 1999). Glaucous-winged Gulls (*Larus glaucescens*) match this pattern in that they are known to prey on adult seabirds and occasionally eat pigeons and kill crows (Jyrkkanen 1975, Verbeek 1988, Hayward and Verbeek 2008), but very few regurgitated pellets contained unidentified passerine remains (Trapp 1979). To the best of our knowledge, there are no reports of identified passerine species preyed upon by Glaucous-winged Gulls. Here we document predation of Glaucous-winged Gulls on Sooty Fox Sparrows (*Passerella iliaca fuliginosa*), Song Sparrows (*Melospiza melodia*), and a European Starling (*Sturnus vulgaris*) on Mandarte Island, British Columbia, Canada.

METHODS

Our observations took place on Mandarte Island, British Columbia, Canada (48° 38′ N, 123° 17′ W). The ~6 ha island hosts a seabird colony (Smith 2006), including ~1,900 pairs of Glaucous-winged Gulls spread over the grassland areas of the island (Blight 2012). The shrub area of the island, consisting mainly of common snowberry (*Symphoricarpos albus*), Nootka rose (*Rosa nutkana*), and Himalayan blackberry (*Rubus armeniacus*) (Smith 2006), provides nesting habitat for ~25 pairs of Sooty Fox Sparrows and 30–50 pairs of Song Sparrows. European Starlings are non-breeding visitors to the island. As part of a long-term study on Mandarte Island, all resident Song Sparrows, and a proportion of the population of Fox Sparrows, are color-banded to allow individual identification (Smith 2006). Since 1975, researchers have studied the population of Song Sparrows on Mandarte Island during spring and summer, and have also opportunistically observed other organisms on the island. We did not conduct systematic studies of gull diet, but report accidental observations, providing new information on components of the diet of Glaucous-winged Gulls.

RESULTS

At 0848 Pacific Daylight Savings Time on 30 April 2011, a color-banded adult male Fox Sparrow was observed singing on an exposed branch of Himalayan blackberry. After the singing bout, the bird took off in a descending flight and flew into the adjacent grassy meadow, passing in front of one of the many standing adult Glaucous-winged Gulls. A standing Glaucous-winged Gull rapidly caught the sparrow mid-flight with its beak and swallowed it whole within ~1 min.

On 23 May 2012, both legs of a Fox Sparrow including its color-bands were found in the

regurgitated pellet of a gull (Fig. 1A). This Fox Sparrow had been color-banded when it was 6–7 days old and weighed 23 g on 11 May 2012. Thus, it would have been an 18–19 day old fledgling when its legs and bands were found. On 29 May 2013, one unbanded leg and some feathers of a Fox Sparrow were found in a gull pellet (Fig. 1B).

In the 1980s, a flying Glaucous-winged Gull snatched a singing male Song Sparrow off its perch (P. Arcese, pers. comm.), and in the mid-1990s a Glaucous-winged Gull caught and swallowed a wet European Starling (L. F. Keller, pers. comm.). Furthermore, two juvenile Glaucous-winged Gulls consumed net-trapped, color banded Song Sparrows in fall 2011 during passive netting sessions, when nets were unattended for less than 5 mins in each instance.

DISCUSSION

Although Glaucous-winged Gulls are known to opportunistically eat adult seabirds, predation on passerines had rarely been recorded and depredated species had not been identified (Trapp 1979). During our observations of Song Sparrows on Mandarte Island, we witnessed predation of Glaucous-winged Gulls on passerines. However, a study by Vermeer (1982) found no bird remains in the pellets of adult and nestling Glaucous-winged Gulls at eight colonies, including the one on Mandarte Island. Our observations thus add to the knowledge of seabird diets. Although Glaucous-winged Gulls on Mandarte Island had not been documented previously consuming sparrows, several other species of gulls have been reported to consume passerines. For example, palearctic gulls prey opportunistically on passerines (reviewed in Glutz von Blotzheim 1999). In North America, American Herring Gulls (*Larus argentatus smithsonianus*) and Great Black-backed Gulls (*Larus marinus*) catch and eat Savannah Sparrows (*Passerculus sandwichensis*) (N. T. Wheelwright, R. Tate, and R. Ingalls in Wheelwright and Rising 2008). Pellets from Ring-billed Gulls (*Larus delawarensis*) in the Great Lakes of North America have also been found to contain remains of six passerine species, including two Song Sparrows (Blokpoel and Haymes 1979), matching with observations of Ring-billed Gulls chasing and capturing songbirds (W. E. Southern in Blokpoel and Haymes 1979). Additionally, there are several online videos of gulls catching adult sparrows (Supplementary Table 1). Although gull predation on passerines had been known to occur, no identified passerine prey species of Glaucous-winged Gulls had been reported. Our observations of predation on three Sooty Fox Sparrows, three Song Sparrows and one European Starling therefore provide examples of some of the costs passerines may experience when living in or near a colony of Glaucous-winged Gulls, although exact quantification of these costs remains speculative.

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Predation of Black-legged Kittiwake Chicks *Rissa tridactyla* by a Peregrine Falcon *Falco peregrinus*: Insights from Time-lapse Cameras

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Peter J. A. Shaw,[1] and Lewis G. Halsey[1]

ABSTRACT.—We directly recorded predation of Black-legged Kittiwake chicks (*Rissa tridactyla*) by a Peregrine Falcon (*Falco peregrinus*) using a remote time-lapse camera. Between 20 July 2013 and 23 July 2013, all four nests in the camera's field of view failed. A peregrine was recorded depredating chicks in two of these four nests. Periods of adult desertion at the other two nests strongly suggests chicks in these nests were depredated as well. Predation happened at night, a rarely documented behavior of the peregrine. Along with giving insights into peregrine hunting behavior, the use of remote cameras allows us to determine nest fate. Determining sources of chick mortality is invaluable for identifying causes of variability in productivity rates of colonial breeding birds.
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Key words: kittiwake, nest fate, nocturnal, Peregrine Falcon, predation, time-lapse camera.

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Nest predation is a major selection pressure in all bird species, influencing a range of life-history traits (Martin 1995). In the absence of ground predators, avian predation can be an important source of breeding failure in colonies of cliff-nesting seabirds (Clode 1993). However, the short lived nature of predation events makes them difficult to observe in conjunction with standard seabird monitoring protocols, which typically involve making visual observations intermittently at optimum stages throughout the breeding season (Walsh et al. 1995). This leads to predation not always being sufficiently considered as a source of mortality when assessing factors influencing colony productivity. By properly measuring predation, the potential bias of attributing nest failure to other factors such as food shortage or environmental change can be reduced (Regehr and Montevecchi 1997).

During the 2013 breeding season, we recorded nocturnal predation on chicks of Black-legged Kittiwakes (hereafter, kittiwakes; *Rissa tridactyla*) by a Peregrine Falcon (hereafter, peregrine;

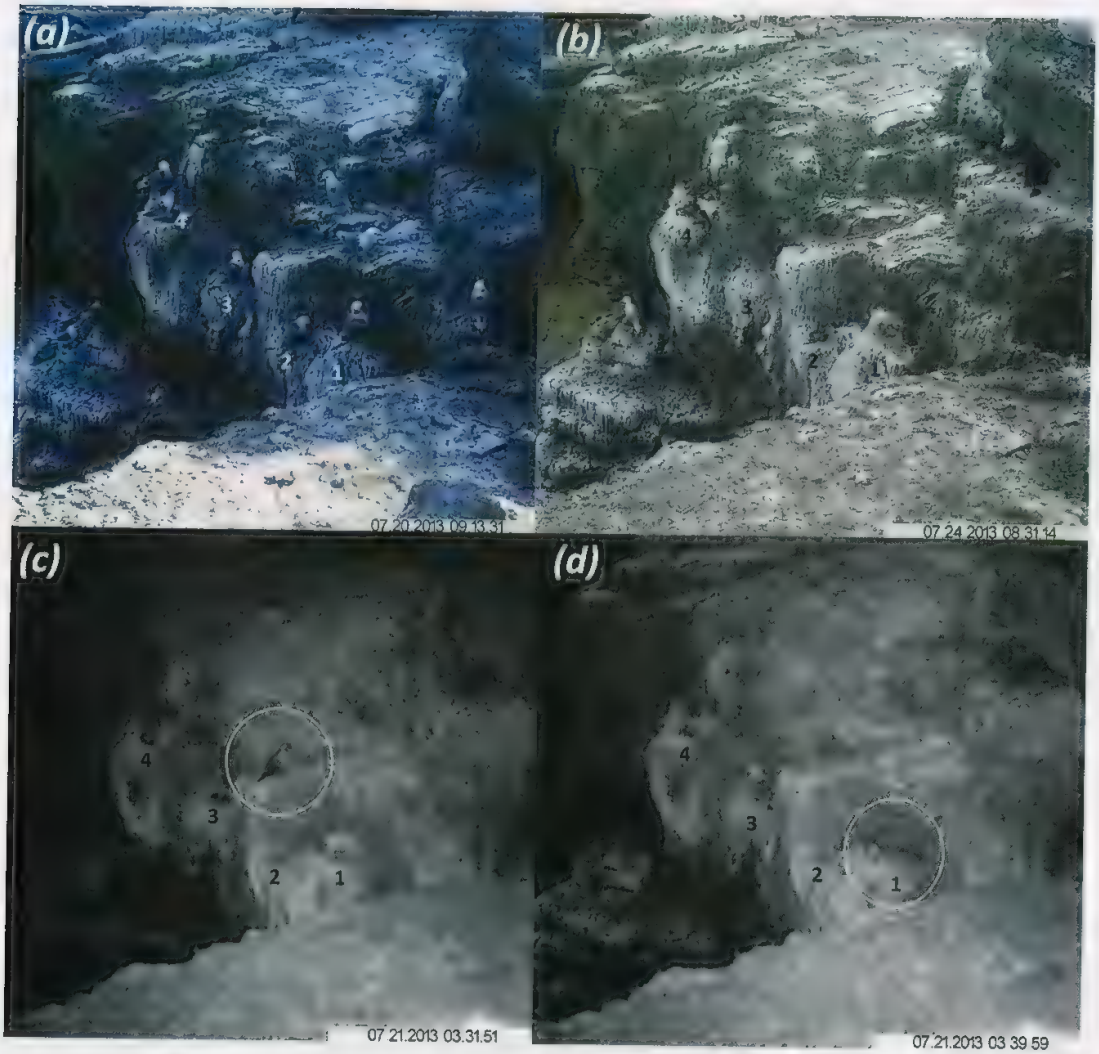

FIG. 1. (a) The study plot 12 hrs before the first predation event, all adults were on at least one chick, the four active nests are numbered. (b) The study plot 1 day after predation (24 Jul 2013), all previously active nests were empty, and the adults have abandoned the site. The bird present towards the left side of the image is not on an active nest. (c) The peregrine (circled in white) at the study site at 0331GMT on 21 July 2013 and shown 8 mins later (d) depredating the chick at nest 1. Note the presence of an adult kittiwake at nest 3. This was the only adult to return when the peregrine was present.

Falco peregrinus) on Puffin Island, North Wales, UK (53° 19′ 05″ N, 04° 01′ 40″ W). The island is situated ~0.6 km offshore and hosted ~385 breeding pairs of kittiwakes in 2013 (Natural Resources Wales, unpubl. data).

As part of a wider study, we deployed five time-lapse cameras (Ltl-Acorn 5210MC) throughout the colony of kittiwakes. One of these cameras was situated close enough to the breeding area to capture clear infrared images which could identify night-time/low-light events. The camera was set to take one image every 4 min, 24 hrs per day. Four active nests were in the field of view of the camera (Fig. 1a).

Between 20 July 2013 and 23 July 2013, all four nests in the field of view of the camera failed (Fig. 1b). The failure was determined by images captured by the camera and further corroborated with human observations made on 26 July 2013. Up until 20 July 2013, these nests were at the chick rearing stage, with nests 1, 2 and 4 containing one chick and nest 3 containing two chicks. At the time of failure, chicks were aged between 4 and 16 days old. Inspection of the remote camera images

identified a Peregrine Falcon directly depredating nests 1 and 3 (Fig. 1c–d). The falcon was observed depredating nest 1 at 0327 GMT (21 Jul 2013) and nest 3 at 0337 (23 Jul 2013), 53 mins and 48 mins before sunrise (0422 and 0425, respectively). The peregrine stayed at nest 1 for between 12–16 mins and at nest 3 for between 16–20 mins.

Predation was not directly observed at nests 2 and 4; however, the behavior of the adult kittiwakes and the sudden disappearance of chicks are indicative of predation. On 20 July 2013 at 2121 (sunset was at 2031), all four attending adults deserted their nests for between 32–36 mins. The image taken at 2121 showed that as well as the adults, the chick in nest 2 was no longer present as it had been at 2117. On 21 July 2013 at 2110 (sunset was at 2029), this happened again at nest 4 with all adults leaving for 21–25 mins, again the chick was no longer visible in the image taken at 2110, whereas it was visible in an image taken at 2106.

It would not have been completely dark during predation events, thus it is possible that the peregrine was using the low-light conditions to enhance its chance of predation success. Hunting during a period of low light is likely to reduce the visual stimulus which would prompt mobbing behavior of neighbouring birds (kittiwakes or large gulls; Chandler and Rose 1988). It could also be that the consecutive nature of the predation events in the present case indicates the peregrine remembered the location of the nest sites. Predation by peregrines at night has been observed before, but only in the presence of artificial light, such as was the case at a Balearic Shearwater colony in Menorca (Wynn et al. 2010), or in cities where artificial light facilitates predation (Rejt 2004, DeCandido and Allen 2006). No predation events were recorded in the daytime.

Productivity of kittiwakes in the UK has been declining in recent years (Joint Nature Conservation Committee 2013). At Puffin Island during the 2013 field season, productivity was notably low; a control plot of 62 apparently occupied nests failed to fledge a single chick. Nests at four other study sites on the island also all failed. A total of nine nests (out of nine) in these other study sites failed during the chick-rearing stage, but the remote cameras were not positioned close enough to record sufficient quality infrared images to determine the cause of the loss. In addition to very low productivity, the timing of breeding was late. The average date of lying was on 13 June, whereas most eggs from colonies of kittiwakes in the UK are laid by the end of May (Coulson 2011). This suggests certain other environmental parameters contributing to a poor breeding season. However by directly recording the peregrine depredating nests on the island, we can consider it as a contributing factor to breeding failure of the birds which did get to the chick-rearing stage. The low numbers of adult kittiwakes that were rearing chicks could have facilitated predation, with low adult density likely failing to provide a strong enough deterrent to predators (Birkhead 1977, Gilchrist 1999).

Although predation of kittiwakes by peregrines has been observed before (Coulson 2011), and has even been speculated to be responsible for colony disappearance (Paine et al. 1990), the importance of such predation is largely unknown. Great Skua (*Stercorarius skua*) and larger gull species are also known to depredate kittiwake chicks, with the impact of such predation considered previously (Furness 1981, Massaro et al. 2001). Identification of causes of mortality allows decoupling of the potential pressures acting upon populations. This not only allows us to quantify predation pressures but also allows a more robust quantification of other drivers which may be acting upon a population.

While seabird predation by avian predators is accepted widely, we suggest that the use of remote cameras provides the possibility to identify and even quantify the occurrence of such events. Nest predation has been recorded successfully in other groups of birds (Cutler and Swann 1999), yet perhaps because of their often remote location, seabird studies are lacking in this respect. In this study, we have demonstrated an approach to document nest predation of a seabird and, in the process, have also captured images that give insight into the behavior of a top predator.

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Predation by a Sharp-shinned Hawk on a Ground-nesting Bird, the White-throated Sparrow

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ABSTRACT.—Predation at the nest is the largest source of reproductive failure for many species of passerine birds, and so it is important that we understand the details surrounding such predation events. With the advent of small video and temperature recorders, nests can now be monitored remotely and predator identity can be assigned. Using remote data collection techniques, we report the unusual observation of a White-throated Sparrow nestling being taken by a juvenile Sharp-shinned Hawk. Normally, Sharp-shinned Hawks focus their efforts on fledgling birds; however, if they do take nestlings, they tend to be from arboreal-nesting species. Since the White-throated Sparrow is a ground-nesting passerine, we suspect that a combination of nest location, nest structure, vegetation structure within the territory, and age of the nestlings made this nest an ideal target for an opportunistic young Sharp-shinned Hawk.
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Key words: nestling, predation, Sharp-shinned Hawk, temperature-logger, video, White-throated Sparrow.

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Predation is the principal source of nest failure in passerine birds (Ricklefs 1969), accounting for well over 95% of all nest failures in some species (e.g., Zanette and Jenkins 2000). Since nestling predation is linked to such massive decreases in fitness and is a significant selective force shaping the evolution of avian life histories, predation at the nest warrants further in-depth research (Martin 1987, 1995). Several studies have documented the effects of nest predation on natural avian populations (Ricklefs 1969; Martin 1993, 1995; Martin and Clobert 1996; Weatherhead and Blouin-Demers 2004), and some researchers have even used artificial nests to ascertain predation rates (Willebrand and Marcström 1988, Whelan et al. 1994, Major and Kendal 1996, Marini and Melo

FIG. 1. Video stills of the Sharp-shinned Hawk depredating a White-throated Sparrow nestling. A) The hawk lands on the nest cup and seems to be aware of an object that is the video camera. B) The hawk continues to scan the area before taking a nestling.

1998, Sloan et al. 1998). Together, these studies show differences in nest predation according to nest placement, concealment, parental response, and various anthropogenic effects such as odor, vegetation disturbances, and fragmentation (Martin 1993, 1995; Robinson et al. 1995; Song 1998; Martin et al. 2000).

Despite these advances, past studies were rarely able to determine the specifics about predator identity and the various events that actually occurred at the nest site during predation, thereby leaving a major gap in our knowledge and preventing us from fully understanding the relationship between predator and prey (Weatherhead and Blouin-Demers 2004). More recent studies on artificial and natural nests have used video cameras to reveal specific details about nest predation (Pietz and Granfors 2000, Stake and Cimprich 2003, Weatherhead and Blouin-Demers 2004, Coates et al. 2008). Still, because this technique is relatively time-consuming, there are gaps in our knowledge about the prevalence of certain predators within and between habitat types. Here, using video cameras at the nest, we report an unusual predation event at the ground-nest of a White-throated Sparrow (*Zonotrichia albicollis*) by an accipiter, the Sharp-shinned Hawk (*Accipiter striatus*).

METHODS

We study a population of White-throated Sparrows at the Cranberry Lake Biological Station (CLBS) in the Adirondack region of upstate New York (44° 81′ N, 74° 87′ W) from early May until mid-August. The CLBS study site is approximately

2 km^2 and supports over 100 breeding pairs of White-throated Sparrows. Territories in the study site are located in historical areas along a beaver meadow, in a bog, and along the edges of small ponds (Tuttle 2003, Formica et al. 2004).

Female White-throated Sparrows nest on or near the ground in small shrubs or grass tussocks. Nests are found by random search or by observing the behavior of paired individuals. Once nests are located, they are checked every other day. To record activity at the nest, video taping with a Sony Handycam model DCR-SX63 camera occurs between 0600–1200 Eastern Daylight Time (EDT) and recording lasts for a total of 120 mins; each nest is recorded once a day. Videos are analyzed for parental and nestling behaviors using JWatcher version 1.0 (Blumstein and Daniel 2007). In addition, a Thermochron iButton (Dallas Semiconductor, TX), set to read at 1-min intervals, is placed in each nest cup to remotely record temperature, incubation/brooding behavior, fledging, and predation events.

RESULTS

On 21 July 2012 while videotaping the nest of a white male X tan female pair (see Tuttle 2003) adjacent to a beaver pond, a juvenile Sharp-shinned Hawk was recorded partially depredating a nest, removing one of the three nestlings. The video was taken at 0723 EDT and lasted until 0842 EDT, with the hawk arriving at the nest at 0800 EDT. No adults were near the nest at this time, with the last feeding trip prior to the hawk's arrival being 3 mins, 11 secs earlier. The nest contained three nestlings, two were 6 days post-hatch, while one was 5 days post-hatch. White-throated Sparrow chicks typically fledge from the nest between days 7 and 12 post hatching (Lowther and Falls 1968).

The video camera had been placed ~3 m from the nest and a few branches from a nearby shrub had been moved to the side to provide a clear view with minimal obstructions. The Sharp-shinned Hawk approached the nest from behind the camera (west). The movement of the bird suggests that it either hopped into the frame or dropped from a close perch but not from a lengthy flight. After multiple movements towards the nest, the hawk retrieved one of the chicks and promptly dropped it near its feet and out of sight of the camera. For 40 secs, the hawk scanned while on the ground and then moved in a walking/hopping motion off view of the camera to the south. The hawk was filmed for a total of 1 min, 29 secs.

After the Sharp-shinned Hawk moved off-camera, nearby vegetation could still be seen moving and occasional vocalizations from the taken chick could be heard. After 33 secs, the hawk flew away from the camera but was still close enough so we could hear soft squeaks from the nestling. The first alarm call by a White-throated Sparrow occurred 15 mins after the flight of the hawk. These chip notes continued for almost 2 mins when again a bird, presumably the hawk, flew away from the camera. An additional 2 mins after the flight noise, the female White-throated Sparrow arrived at the nest cup.

The female sparrow arrived with no food for her offspring and immediately began tremble thrusting (Hartshorne 1962, Haftorn 1994) and maintaining the nest cup. She continued these acts for 7 mins with occasional scanning and short (>10 secs) bouts of brooding and preening. Shortly after, the female left the cup again and the video came to an end. At no point during the predation event or afterwards was the male observed and at no point were two White-throated Sparrows heard simultaneously. However, at various times during the video a male White-throated Sparrow could be heard singing in the distance and the lack of males in adjacent territories would suggest it is the social father of the partially depredated nest.

The juvenile hawk observed in the video captured a single nestling that had a mass of 13.35 g. It was the smallest of the nestlings in mass and tarsus length, and was a full day younger (day 5 post-hatch) than its nest mates. According to Storer (1966), this mass would fall within the range of masses for prey items that are commonly consumed by Sharp-shinned Hawks of both sexes, but especially males. The sex of the hawk is not apparent from the video.

When we checked the nest on the next day (day 7 post-hatch), the remaining two chicks were also gone. Analysis of the Thermochron data indicates that the nest went cold, indicating complete loss, at 1937 EDT on 21 July 2012, almost 12 hrs after the original predation event. We do not know the identity of the predator for these two nestlings; however, we suspect that the Sharp-shinned Hawk had returned to the nest to claim these "easy" prey items.

DISCUSSION

In 25 years of study and over 500 hrs of video at nests, this is the first time we have documented predation of a White-throated Sparrow nestling by an accipiter, the Sharp-shinned Hawk. As it is a small raptor, the Sharp-shinned Hawk feeds primarily on small birds and is known to prefer the canopy of contiguous forests patches (Reynolds and Wright 1978, Reynolds and Meslow 1984, Wiggers and Kritz 1991). Although Sharp-shinned Hawks are opportunistic hunters (Storer 1966, Delong et al. 2013) and are adept at capturing young birds (Quinn 1991) in the forest canopy (Craighead and Craighead 1956, Joy et al. 1994), they usually focus their efforts on fledgling birds, not nestlings (Joy et al. 1994). The few reports that do exist of predation on nestlings by Sharp-shinned Hawks have been on arboreal nesting species rather than those species that nest on or near the ground (McCallum and Hannon 2001, Dunn and Hall 2010), perhaps because arboreal nests are easier to reach and more conspicuous to an accipiter. The well-concealed nests of ground-nesting birds may normally hinder predation by hawks.

There is some suggestion that the likelihood of predation by hawks may be habitat-dependent. For example, in boreal habitats, Sharp-shinned Hawks were found to be responsible for approximately 24% of predation in video-monitored nests (Ball et al. 2009). However, other studies of boreal nesting songbirds found no such association (Sloan et al. 1998, King and DeGraff 2006), with the Sharp-shinned Hawk not being recorded as a nest predator. These latter studies were conducted in the northeastern United States, whereas the former study (Ball et al. 2009) was located in the boreal forests of western Canada. Such inconsistencies may be because of subtle geographic differences in habitat or in hawk life-histories. Our study site in Cranberry Lake, New York is in the most southeastern part of the northern boreal forest, and so the low incidence of hawk predation we observed is consistent with this reported pattern.

In this case of nest predation, both White-throated Sparrow parents seemed unaware of the hawk predator at their nest. The nestlings were quite old at 5–6 days post-hatching, and as such, they required less brooding and more food so it was not unusual that the parents were away from the nest. In addition, since this was the nest of a white morph male, which are considered to be less parental than tan morph males (Tuttle 2003), it was not unusual that the male was not near the nest at that time. White-throated Sparrow parents, particularly tan morph males paired to white morph females, can successfully defend their nestlings from smaller predators such as snakes if they are aware of an attack. In such cases, the parents make vocal alarm calls (chips) and physically attack the predator. If the parents encounter larger nest predators, they still try to drive it away by chipping and flying at the predator; however, they are rarely successful at driving it away. In the case described here, it would have been interesting to see the interaction between the Sharp-shinned Hawk and the White-throated Sparrow parents had they been aware of the attack.

It is possible that we initiated this encounter by exposing the nest when we pulled back one branch to make videotaping easier; however, our movement of the surrounding vegetation was minor. We suspect that the location of the nest within the territory (i.e., in an open area but near a large tree), the angle of the nest cup within the bush (i.e., relatively open), and the vegetation structure of the territory itself made this nest an ideal target for the opportunistic young Sharp-shinned Hawk. In addition, the nestlings were at an age when they were themselves thermoregulatory, and so their own movements would have increased, drawing the attention of a hawk perching in the trees above the nest.

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Fifty One Degrees and 14 Years of Separation: a Trans-Atlantic Recapture of a Banded Leach's Storm-Petrel

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ABSTRACT.—A Leach's Storm-Petrel (*Oceanodroma leucorhoa*) initially banded on Tenerife, Canary Islands, Spain in October 1995 was recaptured on Bon Portage Island off the south tip of Nova Scotia, Canada in August 2009, 13 years and 10 months later, and some 4,660 km and 51° longitude away. Recoveries on breeding areas of seabirds that were originally banded on wintering areas are exceedingly rare. This record appears to constitute the first winter-summer recapture of a Leach's Storm-Petrel.

Key words: Nova Scotia, Procellariiformes, seabird, Spain, Tenerife, winter-summer recapture.

Most banding efforts of seabirds in North America occur on breeding areas. Of seabirds that are banded, the vast majority are recaptured <100 m from their original banding location, whereas far <1% of banded birds are recaptured at locations more than a few kilometers away (Gaston et al. 2008; also see Brewer et al. 2000, Rimmer and McFarland 2001). Thus, progress in understanding long distance movements have been very slow for many seabird species. Although use of modern data loggers has improved our knowledge about movements for some species (e.g., Stutchbury et al. 2009), relatively little information exists on movements of species that weigh <50 g, primarily because data loggers have been too heavy. Although developments in reducing weight and increasing battery life continue, data loggers still are not suitable for all birds (Bridge et al. 2011). Hence, the combination of unequally distributed seasonal banding effort and technological constraints have yielded limited information about movements of small migratory birds initially marked on their wintering grounds (but see Dowell and Robbins 1998, Woolfenden et al. 2001, Ewert et al. 2012). Of over 67,000 Leach's Storm-Petrels (*Oceanodroma leucorhoa*) banded in Canada between 1955 and 1995, fewer than 10 (<0.02%) were ever found outside of Canada (Gaston et al. 2008). In this paper, we describe a winter-summer recapture of a Leach's Storm-Petrel.

METHODS

Bon Portage Island (Outer Island on some maps), Nova Scotia, Canada (43° 27′ N, 65° 44′ W) supports an estimated 50,000 pairs of breeding Leach's Storm-Petrels (MacKinnon 1988, Oxley 1999, DS, unpubl. data). This population has been researched intermittently since the late 1980s (MacKinnon 1988, Oxley 1999, Paterson and Snyder 1999); intensive study of up to 500 nest burrows has been conducted annually since 2005 (O'Dwyer et al. 2008, Mills 2011). As part of a larger research program on reproductive ecology of Leach's Storm-Petrels on Bon Portage Island, we attempt to have all adults in monitored burrows banded.

RESULTS

HLL and EJV retrieved an adult Leach's Storm-Petrel from a burrow on 14 August 2009. The bird bore the Spanish band T.000902. The band was in good condition. On that date, it had the following measurements: 16.6 mm culmen, 159 mm wing chord, 80 mm tail length, and 44.4 g mass. A small blood sample was taken for sexing; molecular testing determined it was a female. An egg was present in the burrow and hatched several days later. This petrel has not subsequently been recaptured or observed on the island. The marked burrow in which it was found was not used in 2010, 2012, or 2013; it was active in 2011, but only one adult was captured and this was not T.000902. In September 2009, band details were provided to the Canadian Wildlife Service (CWS) Banding

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FIG. 1. Leach's Storm-Petrel recovered onshore on Tenerife, Spain in October 1995. The bird was recaptured 4,660 km away in Nova Scotia nearly 14 years later.

Office. In November 2011 we received correspondence from Spain (via CWS) indicating that this petrel had originally been banded on 13 October 1995 off the African coast, on Tenerife, Canary Islands, Spain (28° 33′ N, 16° 20′ W), a straight-line distance of 4,660 km (covering 51° longitude) between banding and recapture locations.

Further correspondence (K.W. Emmerson, pers. comm.) yielded additional information on this bird's history. After a storm in October 1995, a single incapacitated Leach's Storm-Petrel was found on the shore near Garachico, Tenerife, Canary Islands, Spain (Martin and Lorrenzo 2001) and transported to the Tenerife Cabildo Centro de Recuperatión de Fauna Silvestre (CRFS). It was banded (T.000902) and photographed (Fig. 1) immediately before release a few days later, near Bajamar, an area close to a small breeding colony of European Storm-Petrels (*Hydrobates pelagicus*) and Band-rumped Storm-Petrels (*Oceanodroma castro*). The closest populations of breeding Leach's Storm-Petrels are several hundred kilometers north in the United Kingdom (BirdLife International 2012). The blue-gray tone of the plumage in the photographs suggested it was a hatch year bird (Miles 2010). The next known

encounter of T.000902 was our recapture on Bon Portage Island, 13 years, 10 months later.

DISCUSSION

Aside from the unlikelihood of a single bird banded on a wintering area being recaptured at a putative natal site, additional factors make this recapture even less likely. First, as is the case for most migratory birds, mortality of young Leach's Storm-Petrels is disproportionately high early in life. For example, a 40-year study on Kent Island, New Brunswick encountered only ~1% of Leach's Storm-Petrels banded as nestlings (Huntington et al. 1996), although to what extent natal dispersal (*sensu* Greenwood and Harvey 1982) accounted for this low encounter rate is unknown. Several weeks after parents leave the colony, fledgling Leach' Storm-Petrels depart natal sites in September–October to initiate fall migration to their wintering areas. Atlantic populations are assumed to migrate to coastal Europe, down the west coast of Africa, then westward to the east coast of South America, before turning north and returning to breeding areas (Huntington et al. 1996). Young birds spend 4–5 years at sea before eventually breeding (Huntington et al. 1996). T.000902 likely hatched on or near Bon Portage Island, and was blown onshore in Tenerife during its fall migration in 1995. Although we are not completely sure the bird was in its first year, it is generally known that young birds are often more vulnerable to environmental vagaries during migration (Newton 2006), and the photographic record is consistent with this interpretation of T.000902's history. Accepting that this bird was in a weakened state and that it was probably young, its survival probability and thus the likelihood of recapture was already diminished. Recaptures of juvenile seabirds are usually infrequent (Sanders et al. 2010). The fact that this was the only Leach's Strom-Petrel found and banded on Tenerife that year and found again on Bon Portage Island is exceptional. This species is rarely found onshore anywhere in Europe (BirdLife International 2012). Occasional exceptions are 'storm-wrecked' individuals when relatively large numbers may be observed. For example after the 'great storm' in the United Kingdom in 1987, MBL saw several in the county of Surrey, and other reports have appeared in the literature (e.g., Flood 2009). Although information about long distance movements by birds is rapidly becoming the domain of modern data loggers, there will still be instances of valuable data that can be obtained from banding operations, particularly for small species.

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NEW BOOK REVIEW EDITOR FOR THE WILSON JOURNAL OF ORNITHOLOGY

John Faaborg has taken over as book review editor for the *Wilson Journal of Ornithology*. Faaborg has been a member of the Wilson Ornithological Society since 1964. He served as editor of *Ornithological Monographs* for a few years, along with a stint as President of the American Ornithologists' Union. He is close to retirement as a professor at the University of Missouri-Columbia, where he has worked since 1975.

Faaborg sees the provision of book reviews as a society-wide process, with the need for lots of volunteers. He would be delighted to hear from any of you who would like to serve as book reviewers, with information on how you can be reached and what sorts of topics you like to cover in books. Faaborg also may periodically solicit the WOS membership to ask for volunteers for specific books.

Faaborg feels that despite the shift to electronic printing, books will always be an important contribution to the ornithological literature, so it is important to review them for the WOS membership. In fact, as our reliance on electronic means of publication increases, book reviews may become more and more important to be sure that ornithologists are aware of this form of publication. So if you are interested in being a book reviewer for WOS, let John know. He can be reached at faaborgj@missouri.edu. His postal address is:

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Ornithological Literature

John Faaborg, Book Review Editor

IMPERIAL DREAMS: TRACKING THE IMPERIAL WOODPECKER THROUGH THE WILD SIERRA MADRE. By Tim Gallagher. Altria Books, New York, New York, USA. 2013: xxiv + 277 pages. ISBN: 978-1-4391-9152-1. $26.00 (hardcover).—Tim Gallagher is editor-in-chief of *Living Bird*, the popular magazine published by the Cornell Lab of Ornithology, and a self-professed "ghost bird" obsessive. In an earlier book, he documented his search for the Ivory-billed Woodpecker (*Campephilus principalis*; *The Grail Bird*, 2006, Houghton Miflin Company, New York). In his latest book, he indulges his obsession by searching for the Imperial Woodpecker, largest woodpecker in the world. Similarities between the two books abound: a large woodpecker tied to a diminished supply of old-growth trees, a widespread belief that the bird is extinct, a stack of historical records, and a cast of colorful characters who claim to have seen the bird. But there is one significant difference: while the search for the Ivory-billed Woodpecker was conducted in the sleepy bayous of America's Deep South, the search for the Imperial Woodpecker (*Campephilus imperialis*) takes place in what is arguably the most dangerous place in North America, Mexico's Sierra Madre Occidental. What makes this mountainous region so extremely dangerous is its popularity as a marijuana- and poppy-growing region patrolled by guards armed with AK-47s. The growers are affiliated with ruthless drug cartels such as Los Zetas, who have no sympathy for disappearing species and no qualms about killing anyone snooping around their crops.

Gallagher's purpose in researching and writing *The Grail Bird* was to document the sightings of Ivory-billed Woodpeckers made by researchers and ordinary folks, many of whom were of a generation that was fading away (the bird had not been reliably seen since the 1940s). Gallagher's inspiration to search for the Imperial Woodpecker, and to write *Imperial Dreams*, was the discovery of a film clip shot in 1956 by dentist William Rhein, who had made several trips to Mexico in search of the Imperial Woodpecker. That shaky, silent, 85-second film of a female Imperial Woodpecker foraging on a large pine is the only known photographic record of the species in life.

A recurring theme in this book is that of the Imperial Woodpecker being just out of reach—a 1940s researcher is guided to an active nest, only to find a dead adult at the base of the tree and two dead nestlings in the cavity, their bodies still warm; a 1962 visit to Mexico by researchers in which a guide took them to a cavity-riddled pine where he had seen Imperial Woodpeckers the previous year, but they found none; eyewitnesses who had seen the woodpecker, but always just a few years prior to being interviewed by researchers, and not since; and Gallagher's own search, in which promising-looking tracts of mature forest turn out to be too dangerous to search.

Another recurring theme is the wild, untamed nature of the Sierra Madre Occidental. At various times it provided a secure home to the reclusive Tarahumara (the native tribe renowned for their ultramarathon running), the outlaw Pancho Villa, Geronimo and other renegade Apaches, and now *narcotraficantes*, the Mexican drug traffickers. The remote country and rough terrain, along with its sometimes dangerous inhabitants offered protection to the Imperial Woodpecker for many years.

That protection faded as the commercial value of the region's large pines was realized. Gallagher implicates logging and indiscriminate shooting as the causes of the Imperial Woodpecker's disappearance, along with subsistence hunting and poisoning. On that final point, he interviewed a local resident who recalled that a forester provided poison in the 1950s to kill Imperial Woodpeckers because of their damage to valuable timber. This local was apparently the only person Gallagher interviewed who mentioned the use of poison; curiously, based on that lone interview, Gallagher concludes that poison could have been "*the* major factor" in the species' decline. A bit more digging into historical records and interviewing of locals might suss out the relative importance of poison and shed more light on the unfortunate loss of this species.

The Grail Bird contains much more detail about background topics—Bobby Ray Harrison, Jim Tanner, and others involved in the search for

one or both species; Gallagher's obsessive pursuit of rare birds; and, of course, the Ivory-billed Woodpecker itself. Gallagher's approach to that book seemed to be that of a journalist—conducting research, following leads, interviewing people. One weakness of the second book is that it did not follow the same course (at least not to the same degree); doing so would have made it more complete and improved the storyline. Even so, the second book is entertaining—while the Ivory-billed Woodpecker book is more detective story, the Imperial Woodpecker book is more adventure tale.

Gallagher is not convinced that the Imperial Woodpecker is extinct; suitable habitat to support this largest of all woodpeckers still exists, but is currently too dangerous to survey. Based on the advice of locals and his own experiences, Gallagher wisely advises that others not make the trip to look for the species. The book's anecdotes about brutal *narcotraficantes* should serve as ample warning for would-be adventurers.

This book fleshes out Gallagher's *Living Bird* article (2011, 30:16–25) and adds color to an article in *The Auk* on which he is a coauthor (M. Lammertink et al., 2011, 128:671–677). Anyone who was intrigued by either of those articles, was fascinated by the Rhein film (available for viewing at the Cornell Lab's website; http://blog.allaboutbirds.org/2011/10/26/see-the-only-known-images-of-the-lost-imperial-woodpecker-video/), or who has a bit of "ghost bird" obsessiveness, will find this book a worthwhile read.—SCOTT W. GILLIHAN, 5405 Villa View Drive, Farmington, NM 87402, USA; e-mail: swgillihan@gmail.com

LOOKING FOR THE GOSHAWK. By Conor M. Jameson. Bloomsbury Publishing Plc, London, England. 2013: 368 pages. ISBN: 978-1-4081-6487-7. $28.95 (hardcover).—There is a saying in German: "Man erkennt den Habicht daran, dass man ihn nicht sieht." It means, "You know the goshawk is there because you don't see it". But is the goshawk really there, hidden deep within the forest, or is the aura of its presence the fanciful hope of those who want it to be there? That is the question Conor Mark Jameson seeks to answer in his new book, *Looking for the Goshawk*. The book chronicles his three year quest to seek out *Accipiter gentilis*, a bird widely rumored to exist in Britain, but rarely seen. Whenever a goshawk is reported, heated arguments erupt over the authenticity of the sighting or credibility of the observer. Even photographs are not enough to dispel doubt, as critics are quick to exclaim, "That is the picture of a female sparrowhawk, not a goshawk!" And as much as some advocates desperately believe in the goshawk's presence, many others wish it wasn't there at all.

Why is the goshawk so easy to dismiss in the British Isles? In the late 1800s, game keepers mercilessly trapped, poisoned, shot and stuffed all raptors; the goshawk was particularly targeted, to the point that the species was systematically extirpated from the United Kingdom and associated islands. In recent years, however, tantalizing reports of goshawks have entered the British birding community…and the sightings are growing in frequency. Where do the reports originate from and who are the observers? Are they really seeing goshawks or some other species of bird-of-prey?

In his worldwide journey to find answers, Jameson uncovers a troubling, underground culture of goshawk fans and foes. On one side, wildlife biologists jealously guard territories and study nests in secret, while birdwatchers crowd forests for glimpses of a rumored "life bird". On the other side, armed game keepers patrol estates, ready to eliminate any avian predator that enters their domain. Researchers band nestling goshawks and track them with telemetry, only to have the birds mysteriously disappear once they disperse from the study site. Despite a century of conservation laws and passionate naturalists, Jameson discovers that little has changed since the Victorian Era.

Read this book with a desire to understand the underlying forces that sway the success or failure of wildlife conservation programs. Explore with the author the tenuous haunts of the goshawk and wonder why the species is so rare in Britain, but common elsewhere in Europe. In places like Berlin, where the goshawk is comfortable among apartment complexes and city parks, residents welcome the bird; in places closer to the author's home, the goshawk is persecuted and hated and strangely absent. The insights of Jameson's book reveal much about the human attitudes toward wildlife. All too often, the natural environment is a byproduct of what one values. Our response to nature can be as elusive and difficult to understand as the goshawk itself, an unsettling truth that Conor Mark Jameson addresses in this literary work.—STACIA NOVY, Department of Biological Sciences, Southern Illinois University Edwardsville, Box 1651, Edwardsville, IL 62026, USA; e-mail: snovy@siue.edu

GIFTS OF THE CROW: HOW PERCEPTION, EMOTION, AND THOUGHT ALLOW SMART BIRDS TO BEHAVE LIKE HUMANS. By John M. Marzluff and Tony Angell. Atria Books, New York, New York, USA. 2013: 320 pages. ISBN: 978-1-4391-98742. $15.00 (paperback).—Birds are often cited as important ambassadors of the natural world and bird watching or birding as a hobby that increases appreciation for ecological connectedness and conservation. That is hopefully true, but as anyone who studies birds in urban areas knows, mentioning crows to homeowners leads to unpredictable turns of conversation. It can produce an admiring tale of crow ingenuity or, just as easily, reactions such as "I hate them, they wake me up in the morning" or "they have killed all my songbirds". This is not a response heard to a mention of robins or bluebirds. On the other hand, most people recognize a crow when they see one and recognize their good guy-bad guy status, even though few understand crows' complex social lives or roles in ecological communities. Thus crows can play an important positive role in how people view and value the natural world—the ultimate gift.

It is against this backdrop that John Marzluff and Tony Angell have set their goal of broadening everyone's appreciation of crows. *Gifts of the Crow* is clearly aimed at the non-specialist and sets out several themes. First, the elements of crows' intelligence are adaptations that have allowed them (and other corvids) to solve problems and succeed in a human-altered world. Second, these abilities are mechanistically underwritten by the structure and physiology of a large, integrative brain that has many functional similarities to our own. Finally, non-specialists or citizen scientists can contribute to our knowledge of crows' behavior and abilities through their careful observations and documented anecdotes. Such observations are important sources of information for scientists. This proposition should be exciting and encouraging to all of us who are backyard naturalists and bird enthusiasts.

Of course, many readers will be scientifically sophisticated—whether scientists or not—and will include specialists in behavior, neurobiology and even corvid biology. For these readers, this book raises a number of interesting issues and as such, can be discussed from multiple perspectives. There is the problem of how precise or how technical to be in describing complex and only partly resolved processes for the non-specialist reader. The use of anecdotes as a source of data, particularly those from non-specialist observers, is another contentious issue among scientists, as Marzluff and Angell note in the Preface. A book like this runs risks and its success in negotiating them also merits some comment.

Gifts of the Crow is structured around the kinds of behaviors for which crows are known in scientific and popular literatures. Informally written and well-illustrated by Angell, it weaves stories of individual crows' behavior with descriptive explorations of underlying events at a neurobiological level and evolutionary or functional interpretations of behaviors. After a glimpse of humans' long history of interacting with and sometimes appreciating crow intelligence (Amazing Feats and Deep Connections), the second overview chapter (Bird Brains No Longer) summarizes a few formal studies of corvid cognition and then orients the reader to the neurobiology of vertebrates and birds in particular, relating neural processes closely to the examples of cognition.

The following chapters are titled somewhat provocatively from a biologist's perspective: Language; Delinquency; Insight; Frolic; Passion, Wrath and Grief; Risk taking; Awareness; and finally a wrap-up chapter, Reconsidering the Crow. In each, the text moves back and forth between charming anecdotal case histories of individual birds and mechanistic neurobiological explanations for the behaviors. The authors also relate "up-close-and-personal" versions of research on corvid learning and problem solving that establish them as socially and intellectually complex animals, cognitively comparable to primates. Sometimes the authors relate how they evaluated the claims of lay observers or they carefully revise the inferences of those observers to demonstrate how a scientist would look for a selectively advantageous function for the behavior in crow terms, rather than assuming an anthropocentric explanation. An example is their discussion of "mourning" where they suggest that birds investigating dead conspecifics get information relevant to risks rather than actually paying last respects. Thus the chapters strive for education at many levels.

How well does this book serve the general reader or the science-oriented non-specialist? Marzluff and Angell are doing what so many more scientists should be doing: communicating to non-specialists about why scientific discovery is interesting personally and globally important—and saying that anyone can contribute.

Wearing the hat of a lay reader who wants a compelling, easily understood narrative, I am not

sure that the movement back and forth between neurobiology, behavioral anecdotes and behavioral research always worked. The behavioral research was much more informally described than the more technical details of neuroanatomy and physiology. Admittedly, there is necessarily a much larger vocabulary to introduce in the case of the neurobiological side. Often a particular story of behavior was forgotten in the more general narrative of what goes on to regulate and integrate inputs to a brain. On the other hand, the authors often summed up their general points and restated the lessons to be taken from their explanations. The many real examples will clearly entertain and be remembered, although sometimes I wondered if the reader would distinguish the actual examples from the frequent extrapolations to what might have been going on. The final chapter provided a strong end to the book for the lay reader.

Reading it as a scientist, I empathized with the problem of how to balance precision of explanations with the need to keep them at a broad level and still apply them directly to specific cases. The enthusiasm of the authors for adding the neurobiological level of explanation is clear, but the sweeping statements were sometime discomforting. Words like "consciousness" and "thinking" and "reason" that are delicately defined and used in the field of animal cognition appear in many places where they are not really needed. For instance, in explaining an example of a crow's escape from danger by flying into a wind but toward the disturbance, the text reads "The bird's brain combines new sensory information with experiences stored over a lifetime and creates reasoned action". Considering what most people think of as "reasoning", I doubt that the term is justified either by what we know or by what it makes a reader believe we know. That said, in many other places, the book succeeds in giving a sense of how complex experienced-based actions rely on neural mechanisms shared across taxa of cognitively sophisticated animals including us.

As mentioned earlier, Marzluff and Angell also challenge the idea that anecdotes and incidental observations by non-scientists cannot usefully be evaluated and used as evidence. While they briefly discuss the fact that they did review and "test" the anecdotes they uncovered, often interviewing multiple people about what they saw and remembered, it is unclear how they would codify a rigorous method for accepting or interpreting these reports. On the other hand, rare events can be important. Marzluff's and Angell's challenge leaves us with many unanswered questions, including the best way in which to engage the many interested non-scientists and use their eyes and ears, recognizing that they may be less biased in some ways than the scientist.

Who should receive a copy of *Gifts of the Crow*? It is relatively short and written in an easy-going, non-technical way. But as suggested above, not every lay reader will be willing to invest time in the passages describing the neurobiological side of corvids' cognitive prowess. So perhaps it is not for your grandmother, unless she is scientifically oriented. For people who enjoy seeing the natural world in new ways, it will be a "good read" and maybe it will produce a few more crow enthusiasts. Personally, I am giving copies to my graduate students, as a takeoff for discussions of the issues raised above: why we should write for people beyond our colleagues; how to do so effectively for different audiences; how to remain scientifically rigorous while being entertaining and compelling; and that pragmatic and philosophical question—whether and how anecdotes have a role in scientific research.—ANNE B. CLARK, Biological Sciences, Binghamton University, Binghamton, NY 13902, USA; e-mail: aclark@binghamton.edu

THE BLUEBIRD EFFECT: UNCOMMON BONDS WITH COMMON BIRDS. By Julie Zickefoose. Houghton Mifflin Harcourt, Boston, Massachusetts, USA. 2012: 355 pages, numerous color plates and half-tone sketches. ISBN: 978-0-547-00309-2. $28.00 (Cloth).—It is not common for a book of this nature, written clearly as a non-scholarly book and including sentences such as "What's wrong, hon?" addressed to a largely immobile and distressed roadside Turkey Vulture (*Cathartes aura*) to be reviewed in a scholarly journal of ornithology, but this one certainly deserves to be. For those who may not know her, Julie Zickefoose is an accomplished writer, bird artist, licensed wildlife rehabilitator, speaker, conservationist, and regular contributor to National Public Radio. Rarely has such a combination of talent come together so effectively in one human being. Though educated in traditional science at Harvard University, Zickefoose does not consider herself to be sufficiently trained in scientific ornithology to call herself an ornithologist. This view, in my opinion, is technically

correct and absurdly misleading. Just as Barbara McClintock was described by Evelyn Fox Keller (1983, Henry Holt & Co., NY) as having "a feeling for the organism" (in McClintock's case maize), Zickefoose conveys a wondrously insightful understanding of what birds really are and why they matter. No one remotely interested in birds will fail to learn much from reading the book's twenty-five chapters, each of which is essentially devoted to one bird species, most, but not all, common species. I would guess that any hardcore field or laboratory ornithologist who reads this book will come away with a surprising number of insights about the creatures we find so compelling. Indeed, if you have friends or relatives who do not really understand the fascination that we ornithologists have for our subjects, this book would really help bridge that gulf.

The book's title, "the bluebird effect," obviously derives from chaos theory, "the butterfly effect," where a small atmospheric change (such as could be caused by the flapping wings of a butterfly) can subsequently multiply into a major effect, such as a tornado. In Zickefoose's usage, it refers to how she came, quite by accident, to care for and release a male Eastern Bluebird (*Sialia sialis*) that subsequently lived in one of her bluebird boxes for eight years and fathered at least sixty-seven young in that time period, all under Zickefoose's careful observation. That initial interest in this single bird that she named Mr. Troyer, her experience with it and the rest of the "Troyer family," was catalytic in Zickefoose's burgeoning career in bird rehabilitation, observation, and insight.

Yes, she names some of "her" rehabilitated and released birds. As she explains, "I need to name them if I'm to release them and keep track of them afterward. Naming them honors their distinct personalities, proclivities, and idiosyncrasies. Mostly though, I need to name them because I'm their mother" (p. 79). If, because of that, you are tempted to conclude that this book is yet another anthropomorphic romp away from real science, you are very mistaken. Zickefoose's empathy for her subjects does not cloud her observation skills. Quite the contrary, it seems to sharpen them. As Zickefoose states with regard to how she perceives wildlife rehabilitation: "We're anything but bunny huggers; we need to be flint-hard at the core. We do what it takes to get these birds out the door and back into the wild, and we're not going to fall down on the job just before the finish line. There's too much invested. The reward is in understanding how a bird thinks, how it develops, and how it might react to any given situation; "It's an understanding so deep that it goes beyond words" (p. xxii).

Zickefoose effectively engages the reader in the complexity of avian conservation issues in several chapters, one of which focuses on her earlier work, began in 1981, on conservation of Piping Plover (*Charadrius melodus*) and Least Tern (*Sternula antillarum*) populations in Connecticut (while she was associated with The Nature Conservancy). She relates how, as but one individual without any real authority (it was not until 1985 with the decision to confer endangered species status on the Piping Plover that federal and state protection was guaranteed), she organized teams of largely female volunteers to rope off and patrol the tern colonies and plover nesting areas all along Connecticut's coastal beaches, attempting to protect the birds from the public. She actually issued toy sheriff badges to her volunteers, each of which she asked to dress in khakis to look more authoritative as they tried to "exert their authority" to keep people out of the birds' nesting sites. While doing so Zickefoose compiled much data on plover and tern nesting success and factors that resulted in nest failure. After determining that three Black-crowned Night-Herons (*Nycticorax nycticorax*) were essentially annihilating a Least Tern colony on Menunketesuck Island in Connecticut, Zickefoose decided she had little choice but to eliminate the night-herons and ultimately did so by strapping tiny "backpacks" containing the poison Avitrol on the backs of tern chicks. The predators ate the chicks, quickly died, and the problem was solved. But in relating this example, Zickefoose explains the reality of what hard core conservation decisions really mean in terms of the need to control some species so that others may thrive (or at least have a chance), much of which is ultimately driven by how anthropogenic activities have affected and altered all manner of environmental parameters. It is a chapter most students of conservation biology would find thought provoking.

Zickefoose is a good storyteller. One chapter describes her unique relationship with a female Orchard Oriole (*Icterus spurius*) that was injured by a cat and could never be liberated to the wild. She kept the bird for seventeen years, a record longevity for this species. As she writes, "Seventeen years–who'd a thought I'd still be whipping up sweet potato and butternut squash, three-cheese

ravioli, and fresh fruit every blessed morning?" (p. 221). Another chapter relates how she began putting out crushed eggshells for a group of Barn Swallows (*Hirundo rustica*) that did not nest very near the Zickefoose property. She was driving along some miles away when she observed some Barn Swallows perched on a utility wire. She stopped and looked at them and they looked at her and immediately became airborne and obviously excited as they recognized her. She drove and they flew back to her home (arriving before she did) where, of course, she replenished their supply of crushed eggshells.

Every bird matters in Zickefoose's life. Her chapter on how she managed to raise and release seven orphaned Chimney Swifts (*Chaetura pelagica*) is nothing short of astonishing, as it underscores Zickefoose's determination and innovativeness, to say nothing of her refusal to ever give up on a bird problem. "I mix up my latest avian culinary offering, suggested by Astrid [Astrid MacLeod, a bird rehabilitator]–a scrambled egg, its shell crushed to powder and stirred back in, with two tablespoons of dried insects added for extra protein. Fried up, the bug omelet smells nauseating and looks even worse, a gray mess of bug bits and egg. But they eat it with gusto, and it should have everything they need to grow and thrive. I order $36.00 worth of dried flies and one thousand live crickets online for $16.50. Raising chimney swifts is neither easy nor cheap, but it pays richly in intangibles" (p. 126). These chapters not only describe the nuts and bolts of bird rehabilitation efforts but also abound with rich information about the biology of the subjects. There is much to be learned by knowing birds one at a time, and this book conveys that reality with utter clarity.

Two chapters particularly stand out to this reviewer. The first is a lengthy chapter on Ruby-throated Hummingbirds (*Archilochus colubris*) and the second is the chapter devoted to the Ivory-billed Woodpecker (*Campephilus principalis*).

In the summer of 2003, Zickefoose accepted two downed nests, each containing two tiny, newly hatched Ruby-throated Hummingbirds. She details the Herculean effort required to bring them to the point where three (all males) were successfully fledged. The work involved was staggering but apparently highly rewarding. Zickefoose was required to feed the birds at approximately twenty-minute intervals, which meant that she had to take the tiny broods to the grocery store with her so as not to miss a feeding. She had to lop heads off of mealworm larvae and squeeze the contents out so as to provide adequate protein for the birds. Because the nests were mite-infested she microwaved them to kill the mites. She remodeled a room so that the hummingbirds could have an aviary in which to practice flight and independent feeding. When one was injured (and subsequently had to be euthanized), she kept it for some time in its own glass container, complete with a "handicapped access feeder." Zickefoose describes her life that summer as, "However delightful raising hummingbirds is, it is like being under house arrest" (p. 76). Zickefoose keeps meticulous data on her birds and she notes that the professional literature suggests an earlier independency for newly fledged Ruby-throated Hummingbirds than is the case with the three she raised and released. She suggests that the challenges of field observations make it difficult to accurately determine exactly when birds so difficult to study as hummingbirds do attain true independence. Though Zickefoose does not band her subjects she does know them as individuals. Amazingly, on 17 April 2004, the three male hummingbirds that Zickefoose raised each returned from presumably migrating across the Gulf of Mexico and back. If you are wondering how she knew that these really were the three she raised, read the chapter to its conclusion.

Perhaps no chapter blends Zickefoose's talent for factual writing, storytelling, and for artistic rendering of birds better than when she muses over her imaginary encounter with an Ivory-billed Woodpecker. Though the book is visually appealing throughout, with numerous color paintings and sketches, the Ivory-billed chapter nonetheless stands out. The chapter is adopted from an article Zickefoose published in 1999 and thus deals with none of the more recent discussions and controversy about the Arkansas reports. Instead it is partly a work of pure fiction, where Zickefoose imagines what it might be like to actually encounter an Ivory-billed and, from that, goes on to discuss actual conversations she had with James Tanner, Don Eckelberry, and Jerome Jackson about the sad history of the species and the hope that somehow it may still persist. The chapter is elegantly written.

The key to understanding this book is to take Zickefoose at her word, namely that she sees birds as individuals. Her remarkable ability to so clearly convey her enthusiasm for and understanding of her subjects both in words and in art is something that makes this work exceptional among many generalist books about birds. Zickefoose wears her knowledge

lightly, sharing it with ease and often humor, as when she mentions that she no longer feeds her son breaded chicken nuggets because Turkey Vultures refuse to eat them. This book, or parts thereof, would make a very strong contribution as supplemental reading in many an introductory ornithology course, including mine.—JOHN KRICHER, Biology Department, Wheaton College, Norton, MA, 02766, USA; e-mail: jkricher@wheatonma.edu

A GUIDE TO THE BIRDS OF TRINIDAD AND TOBAGO. By Richard ffrench. Cornell University Press, Ithaca, New York, USA. 2012: xxvi + 407 pages. ISBN: 978-0-8014-7364-7. $39.95 (paperback).—This is the third edition of this guide, with the second edition published in 1991 and the original going back to 1973. I have had a copy of the "revised edition" since it came out in 1976. My copy appears to have been well used in the field, although unfortunately my wife has been to Trinidad while I have not.

This was among the first field guides to any part of South America that was heavily illustrated. Prior to a trip to Venezuela in 1973, I spent a lot of time at the American Museum of Natural History trying to learn the birds of that region from skins. At that time the only book that listed the birds of the area we were visiting (Meyer de Schauensee 1966) was heavily text, with few plates. Although the guide to Trinidad and Tobago was limited to the few hundred species that occur on that land-bridge island, those plates would have been extremely handy to have in the field; however, my trip preceded release of the first edition by just a few months.

One of the things I always liked about this book is that it is a "guide," and not just a "field guide." Thus, it is much more complete in the information provided for each species that has been recorded on these islands in recent history. It goes well beyond the information needed for identification to detailed data on size, weight, food habits, nesting, behavior, and a variety of other traits. It begins with nearly 30 pages that describe the islands involved and the habitats they contain. Perhaps this is easier to do for a region that contains less than 500 species, but it is great for whatever reason. While the text for all editions is mostly the same, the art program for the third edition is extremely expanded. The first edition had only 28 plates, with about a dozen species on each; the latest version has 40 plates, with from 6 to 26 species on each, but usually about a dozen species. The plates cover all species that have been found on Trinidad and Tobago, including migrants and winter residents. This single guide is all one needs for a trip to these islands!

The islands of Trinidad and Tobago are of great interest ecologically because they are land-bridge islands. Just a few thousand years ago they were higher ground along the coast of northeastern South America, which was larger as ocean levels had receded because water was tied up in the ice caps during glacial maxima. Ecologists assume that when these islands were just higher ground on the mainland, they probably supported more land-bird species than they do today; possibly such as one would find on the nearest mountain in northeast Venezuela. As the glaciers receded and ocean levels rose, these highlands became islands, and we assume that many of the resident species went extinct as their populations dealt with the constraints of being on an island. Those that could survive are often more abundant than they are on the more diverse mainland. To me, this suggests that Trinidad would be a great place for the novice who is interested in seeing some tropical birds but does not want to be overwhelmed by the immense diversity on South America. An added feature is that Trinidad seems to be safe and it has a support structure that makes getting there pretty easy, including the famous Asa Wright Nature Center which helped produce this book. Certainly, anyone planning at trip to Trinidad and/or Tobago must have this guide; others may find it a nice addition to their tropical library because of the breadth of natural history information included.—JOHN FAABORG, Division of Biological Sciences, University of Missouri-Columbia, 110 Tucker Hall, Columbia, MO 65211-7400, USA; e-mail: faaborgj@missouri.edu

THE UNFEATHERED BIRD. By Katrina van Grouw. Princeton University Press, Princeton, New Jersey, USA. 2011: 287 pages, 385 drawings. ISBN: 978-0-691-15134-2. $49.95 (hardback).—The Unfeathered Bird is a book perfect for anyone who appreciates both the science and art of avian anatomy. It successfully combines the stunning visual beauty and exquisite attention to detail frequently seen in historical illustrations with a strong familiarity of modern scientific knowledge of avian anatomy. The drawings show birds in natural postures, but with their inner complexity revealed by the removal of feathers,

skin, and often a combination of these in order to better illustrate the astonishing adaptations seen in various groups of birds. The drawings were made from actual specimens and the author went to great lengths to obtain those specimens and use them to produce the most realistic representations possible.

If you expect, or even prefer to see anatomical drawings in stiff, unnatural positions, and with every bone labeled, this is not the book for you. The most important aspects of the bird's anatomy are discussed in the text and quite easily seen in the artwork, which is shown with only a title/description of the bird's scientific name, common name, and a brief description of the preparation. The text that accompanies each group of drawings is relatively free of scientific jargon, making this book accessible to any reader. The text should not be overlooked, as it tells well the story of the drawings and the importance of the anatomy illustrated there.

This work was done over 25 years, truly a labor of love and passion. The specimens were acquired after natural death and then prepared and posed for these incredible drawings. It is difficult to think of looking at birds without their skins and/or feathers as being "life-like," until you read this book and see the drawings for yourself. An American Robin (*Turdus migratorius*) skeleton perched on a branch with an earthworm in its beak, a diving Red-throated Loon (*Gavia stellata*), a Budgerigar (*Melopsittacus undulatus*) peering into a mirror at its reflection, and many more drawings bring these bones to life in a way that is both surprising and beautiful.

The book is arranged into two main parts, the first being a generic introduction to avian anatomy, divided into major regions and accompanied by explanations relating anatomy to evolutionary history and function. The second part is a series of six chapters, each covering a group of birds that are superficially similar to one another. That is, their morphology is similar, whether because of evolutionary relationship, or because of convergent evolution. As a scientist who teaches both bird anatomy and evolution, at first I found this form of division disconcerting, but I soon began to understand and appreciate the logic behind the organization in this particular book. The birds in each group are placed together to make it easier to compare them to one another, and the text which accompanies them does a marvelous job of explaining the origin of the similarities. It is a system which works well in this particular situation. Not all bird groups are covered, though most of the major groups of birds of the world are represented as well as some domesticated species.

I recommend this book for anyone who finds the juxtaposition of science and art both exciting and beautiful. This book makes that beauty accessible and yes, even useful. In the introduction to the book, the author, Dr. van Grouw states, "I've attempted to make The Unfeathered Bird a convergence of art and science, accessibility and erudition, old and new – without compromise and without apology. I hope it finds its niche." I feel confident that it will.—MIA R. REVELS, Northeastern State University, 611 N. Grand Avenue, Tahlequah, OK 74464, USA; e-mail: revels@nsuok.edu

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This issue of *The Wilson Journal of Ornithology* was published on 27 March 2014.

Continued from outside back cover

120 The Life of Alexander Wilson
Edward J. Burtt

Short Communications

121 Time budgets of male Calliope Hummingbirds on a dispersed lek
Richard L. Hutto

128 Feeding rates, double brooding, nest reuse, and seasonal fecundity of Eastern Wood-Pewees in the Missouri Ozarks
Sarah W. Kendrick, Frank R. Thompson III, and Jennifer L. Reidy

133 New Caledonian Crows' (*Corvus moneduloides*) pandanus tool designs: diversification or independent invention?
Gavin R. Hunt

140 Courtship and aggressive behavior of the Least Grebe in the breeding season
André Konter

147 Video evidence of infanticide by a female Red-winged Blackbird
Les D. Murray

151 Breeding records of Black-capped Vireo (*Vireo atricapilla*) in northeastern Mexico
José I. González-Rojas, Craig C. Farquhar, Mario Guerrero-Madriles, Oscar Ballesteros-Medrano, and Adriana Núñez-Gonzalí

155 Observations of Glaucous-winged Gulls preying on passerines at a Pacific Northwest colony
Pirmin Nietlisbach, Ryan R. Germain, and Christophe A. H. Bousquet

158 Predation of Black-legged Kittiwake chicks *Rissa tridactyla* by a Peregrine Falcon *Falco peregrinus*: insights from time-lapse cameras
Philip M. Collins, Jonathan A. Green, Stephen Dodd, Peter J. A. Shaw, and Lewis G. Halsey

161 Predation by a Sharp-shinned Hawk on a ground-nesting bird, the White-throated Sparrow
Adam Betuel, Elaina M. Tuttle, and Rusty A. Gonser

166 Fifty one degrees and 14 years of separation: a trans-Atlantic recapture of a banded Leach's Storm-Petrel
Ingrid L. Pollet, M. Barry Lancaster, Holly L. Lightfoot, Emma J. Vaasjo, and Dave Shutler

169 New Book Review Editor for the Wilson Journal of Ornithology

170 Ornithological Literature
John Faaborg, Book Review Editor

The Wilson Journal of Ornithology

(formerly *The Wilson Bulletin*)

Volume 126, Number 1 CONTENTS March 2014

Major Articles

1 A hard nut to crack: rapid evolution in the Kona Grosbeak of Hawaii for a locally abundant food source (Drepanidini: *Chloridops kona*)
Storrs L. Olson

9 Extra-pair mating and sexual selection on male traits across populations
Linda A. Whittingham and Peter O. Dunn

19 Bird mortality during nocturnal migration over Lake Michigan: a case study
Robert H. Diehl, John M. Bates, David E. Willard, and Thomas P. Gnoske

30 Influence of season and time of day on marsh bird detections
Tyler M. Harms and Stephen J. Dinsmore

39 Retention rates of glue-attached radio-transmitters on two small bird species with contrasting life histories
Kristen M. Diemer, Hazel E. Wheeler, and Joseph J. Nocera

47 Relative abundance of small mammals in nest core areas and burned wintering areas of Mexican Spotted Owls in the Sacramento Mountains, New Mexico
Joseph L. Ganey, Sean C. Kyle, Todd A. Rawlinson, Darrell L. Apprill, and James P. Ward Jr.

53 Home range characteristics of Mexican Spotted Owls in the Rincon Mountains, Arizona
David W. Willey and Charles Van Riper III

60 Vineyard and riparian habitat, not nest box presence, alter avian community composition
Julie A. Jedlicka, Russell Greenberg, and Peter T. Raimondi

69 Do avian communities vary with season in highly urbanized Hong Kong?
Daqing Zhou and L. M. Chu

81 First description of nest, eggs, incubation behavior, and nestlings of Trilling Tapaculo (*Scytalopus parvirostris*)
Chris Smith and Gustavo Londoño

86 Yolk mass variation in White-rumped Swallows (*Tachycineta leucorrhoa*)
Melina Barrioneuvo, Florencia Bulit, and Viviana Massoni

94 Risky edges: temporal variation in brood parasitism of Northern Cardinals
Samantha K. Stoklosa, Laura J. Kearns, and Amanda D. Rodewald

98 Court cleaning behavior of the White-bearded Manakin (*Manacus manacus*) and a test of the anti-predation hypothesis
César Cestari and Marco Aurélio Pizo

105 Food resource exploitation strategies of two reedbed specialist passerines: Reed Parrotbill and Oriental Reed Warbler
Li-Hu Xiong and Jian-Jian Lu

115 Unusual wintering distribution and migratory behavior of the Whooping Crane (*Grus americana*) in 2011–2012
Greg D. Wright, Mary J. Harner, and James D. Chambers

Continued on inside back cover